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La conservation de la biodiversité dans les aires protégées en zones périurbaines: dynamique des communautés végétales au parc national du Mont-Saint-Bruno entre 1977 et 2013

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Résumé

Ce mémoire visait à déterminer si un petit parc périurbain, en l'occurrence le Parc national du Mont-Saint-Bruno, est parvenu à maintenir l'intégrité de sa flore au cours des trente dernières années en dépit de pressions humaines croissantes et de perturbations naturelles passées, en plus d'identifier les principaux changements floristiques survenus au cours de cette période et les facteurs responsables. Pour répondre à ces objectifs, une étude historique a été réalisée, en comparant un inventaire floristique ancien (1977) à un inventaire récent (2013). Mes résultats montrent d'abord une forte croissance de la diversité alpha indigène au cours des 35 dernières années, accompagnée d'un déclin significatif de la diversité bêta (30%). Malgré cette homogénéisation taxonomique, la diversité fonctionnelle de la flore forestière s'est accrue, la rendant probablement plus résiliente aux événements perturbateurs. D'autre part, mes analyses ont révélé la progression de traits fonctionnels souvent associés à des habitats forestiers intensément broutés, révélant une certaine influence du cerf de Virginie sur la composition et la structure de la flore forestière. Enfin, mes résultats ont montré que les herbiers botaniques se révèlent être une alternative fiable aux méthodes traditionnelles pour documenter et évaluer l'impact des grands herbivores sur la morphologie des plantes broutées. Au final, cette étude a montré que les petites aires protégées périurbaines peuvent jouer un rôle majeur dans la préservation de la diversité floristique d'habitats forestiers d'intérêt, particulièrement lorsque leur statut de protection permet d'encadrer de manière stricte les activités humaines.

Mots-clés: Conservation, biodiversité, aires protégées, parc périurbain, diversité bêta, homogénéisation, diversité fonctionnelle, trait fonctionnel, cerf de Virginie, étude historique

Abstract

This study aimed to determine whether a small suburban park, namely the Mont-Saint-Bruno National Park, managed to maintain the integrity of its flora over the last thirty years despite increasing human pressures and past natural disturbances, in addition to identify the main floristic changes during this period and the drivers of observed changes. To do so, a historical study was conducted by comparing past (1977) and recent (2013) floristic surveys. First, a striking increase in alpha diversity, driven mostly by native species and associated with a significant decline (30%) in the beta diversity over the last 35 years was found. Despite this taxonomic homogenization, the functional diversity of forest flora has increased, probably increasing its resistance to disruptive events. Furthermore, analyses revealed the progression of functional traits associated with overbrowsed forest habitats, revealing some influence of white-tailed deer on the composition and structure of the forest flora. Finally, my study also showed that herbarium specimens can be used as a reliable alternative to traditional methods to document and assess the impact of large herbivores on browsed plants morphology. In conclusion, this study showed that small suburban protected areas can play a major role in the preservation of the floristic diversity of rich forest habitats, particularly when their status strictly frames human activities.

Keywords: Conservation, biodiversity, protected areas, suburban park, beta diversity, homogenization, functional diversity, functional trait, white-tailed deer, legacy study

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La Terre n'appartient pas à l'Homme, c'est l'Homme qui appartient à la Terre

Sitting Bull

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Chapitre 1: Introduction générale

La biodiversité mondiale connaît d'importants reculs depuis les dernières décennies, déclin confirmé notamment par l'augmentation du nombre d'espèces menacées d'extinction (Butchart et al. 2010; Barnosky et al. 2011). Pour tenter de contenir cette érosion de la biodiversité, les efforts se portent entre autres sur la création d'aires protégées (Timko & Innes 2009; Cantú-Salazar & Gaston 2010). Des craintes ont néanmoins été formulées quant à la capacité réelle des aires protégées à préserver de manière pérenne l'intégrité de leur biodiversité (Parrish et al. 2003; Terborgh 2004; Craigie et al. 2010; Laurance et al. 2012). En effet, bien qu'elles contribuent à réduire la perte d'habitats (Joppa et al. 2008; Geldamm et al. 2013), leur efficacité à maintenir les populations d'espèces d'intérêt est moins claire (Wiersma & Nudds 2009; Craigie et al. 2010; Laurance et al. 2012; Geldamm et al. 2013). Par exemple, Craigie et al. (2010) ont démontré, entre 1970 et 2005, un déclin de près de 60% dans l'abondance des 589 populations de grands mammifères des 78 aires protégées africaines étudiées.

La taille des aires protégées et le contexte environnant sont souvent suggérés comme étant responsables de ces résultats mitigés. Les aires protégées sont en effet souvent de petite taille, incapables d'assurer la survie d'espèces à grand domaine vital (Laurance 2005; Cantú-Salazar & Gaston 2010). Elles sont également fortement influencées par les activités anthropiques à l'extérieur et à l'intérieur de leurs frontières (p. ex. braconnage, dérangement, pollution) (Chape et al. 2005; Craigie et al. 2010; Laurance et al. 2012), en plus d'être souvent isolées dans une trame paysagère largement fragmentée, favorisant l'introduction d'espèces exotiques (DeCandido 2004) et entravant le mouvement de la faune et de la flore (Cantú-Salazar & Gaston 2010; Laurance et al. 2012). Ce faisant, la pérennisation de la biodiversité est compromise, à un point tel que certaines aires protégées perdent progressivement leur raison d'être (Craigie et al. 2010; Laurance et al. 2012).

Dans un tel contexte, ce mémoire visera à déterminer la capacité d'un petit parc en région périurbaine à préserver l'intégrité de sa flore forestière. Les prochaines sections seront ainsi consacrées aux facteurs responsables des changements floristiques récents observés dans les forêts tempérées de l'Amérique du Nord, avec une emphase particulière sur ceux susceptibles d'avoir influencé la composition et la structure des communautés forestières du parc national du Mont-Saint-Bruno, le présent objet d'étude. Par la suite, la situation particulière des écosystèmes et des aires protégées en région périurbaine sera exposée. Enfin, l'intérêt des études historiques dans la compréhension des dynamiques écologiques actuelles sera démontré.

1.1 Facteurs de changement dans les forêts tempérées nord-américaines

Au cours des dernières années, plusieurs études ont montré que les écosystèmes forestiers des régions tempérées de l'Amérique du Nord étaient fortement influencés par l'urbanisation et la fragmentation de l'habitat (McKinney 2002, 2006; McCune & Vellend 2013), la prolifération d'espèces exotiques (Wiegmann & Waller 2006; Vavra et al. 2007; Pereira et al. 2012), les perturbations naturelles (Rogers et al. 2008; Li & Waller 2015) et l'accroissement des populations de cerfs de Virginie (Côté et al. 2004; Rooney 2009; Holmes & Webster 2011). À titre d'exemple, l'étude des changements survenus sur une période de 60 ans dans 62 forêts du nord du Wisconsin et de la péninsule nord-ouest du Michigan révèle que les espèces exotiques, les graminées et les cypéracées ont progressé au cours des décennies au détriment des espèces indigènes, en raison notamment des pressions de broutement exercées par le cerf de Virginie (Wiegmann & Waller 2006). Plus récemment, l'étude de l'évolution de la flore de la portion sud de l'île de Vancouver (1968-2009), marquée par une rapide urbanisation au cours des 40 dernières années, rapporte que la diversité locale a considérablement augmenté en raison de la progression d'espèces exotiques et d'espèces indigènes tolérantes aux perturbations (McCune & Vellend 2013).

Parmi ces facteurs, trois feront l'objet d'une attention particulière, étant susceptibles d'avoir influencé la composition et la structure de la flore et des peuplements forestiers du parc national du Mont-Saint-Bruno, soit la surabondance de cerfs de Virginie, les plantes exotiques et la fragmentation de la canopée par le verglas de 1998 et la création de sentiers pédestres.

1.1.1 La surpopulation de cerfs de Virginie: une atteinte à la biodiversité

En Amérique du Nord, la rapide augmentation du nombre de cerfs de Virginie (*Odocoileus virginianus*), au cours du siècle dernier est le résultat de l'adéquation de plusieurs facteurs, notamment (i) la transformation des habitats forestiers en champs agricoles ou en friches forestières (plantations, etc.), (ii) l'imposition de règlements de chasse plus restrictifs et (iii) la diminution drastique des prédateurs naturels (Côté et al. 2004). Ces facteurs ont ainsi contribué à accroître les ressources alimentaires de ce grand herbivore, tout en réduisant les mécanismes de régulation des populations, menant aujourd'hui à des densités locales très élevées. Ces densités dépassent même parfois la capacité de support des écosystèmes forestiers tempérés (c.-à-d., le nombre de cerfs qu'un habitat peut supporter de manière durable), estimée à moins de 8 cerfs par km^2 (Alverson et al. 1988; Horsley et al. 2003). C'est le cas notamment du parc national du Mont-Saint-Bruno. Or, la surabondance de cerfs de Virginie peut bouleverser profondément l'équilibre

des écosystèmes forestiers, puisque le broutement entraîne des impacts allant de l'échelle de la plante à l'ensemble de la communauté forestière.

1.1.1.1 Les impacts du broutement à l'échelle de la plante

Le cerf de Virginie peut menacer directement la croissance, la reproduction et la survie des plantes qu'il consomme en affaiblissant leur métabolisme par le broutement des feuilles, bourgeons, jeunes pousses, fleurs et fruits (Rooney & Waller 2001, 2003; Côté et al. 2004). Suite à des épisodes de broutement répété et intense, une modification de leur morphologie peut même s'ensuivre (Rooney 1997; Knight 2003; Shelton et al. 2014). C'est le cas par exemple du trille blanc (*Trillium grandiflorum*), qui tend à être de plus petite taille et moins enclin à fleurir lorsque soumis au broutement répété du cerf de Virginie (Anderson 1994; Augustine & Frelich 1998; Knight 2003). La population tend à être dominée par de petits plants végétatifs et dépouillée de plants à haut succès de reproduction (Rooney & Gross 2003; Knight 2007). À terme, le broutement récurrent peut même causer le déclin drastique, voire l'extinction des populations de trilles blancs (Rooney & Gross 2003; Knight et al. 2009).

Les plantes peuvent avoir diverses stratégies de réponse au broutement. Certaines, dites résistantes, ont développé des mécanismes de défense morphologique (épines, tissus calcifiés, etc.) ou des stratégies de repoussement (p. ex. des composés secondaires réduisant la digestibilité de la plante, comme les phénols et les alcaloïdes) (Aber & Melillo 2001; Côté et al. 2004), tandis que d'autres, dites tolérantes, parviennent à supporter certains préjudices sans pour autant voir leur croissance ou leur survie compromises (Côté et al. 2004; Hester et al. 2006). Certains traits fonctionnels accentuent la tolérance à l'herbivorie en maximisant les chances de survie de la plante broutée. Par exemple, la présence d'un méristème basal, comme chez les graminoïdes, assure la production de nouveaux tissus suite à un épisode de broutement, étant inaccessible aux brouteurs (Coughenour 1985). De la même façon, la présence de structures de réserve souterraines (rhizome, tubercule, etc.) permet d'emmagasiner de l'énergie pour soutenir un broutement répété (Rooney & Waller 2001; Frerker et al. 2013), alors qu'une petite stature réduit les probabilités de sélection par un brouteur (Coughenour 1985; Anderson 1994; Frerker et al. 2013; Shelton et al. 2014). Les fougères sont aussi généralement ignorées par les cerfs, étant peu comestibles (Rooney 2009) et pauvres en nutriments (Wiegmann & Waller 2006). Néanmoins, lorsque la pression de broutement se poursuit intensément sur plusieurs années, même les espèces tolérantes peuvent décliner de manière drastique (Knight 2003; Knight et al. 2009).

1.1.1.2 Les impacts du broutement sélectif à l'échelle de la communauté

Le broutement par les grands herbivores agit à l'échelle de la plante, mais également à l'échelle de la communauté entière, par le biais d'impacts indirects et conjugués. D'abord, le cerf de Virginie évite les plantes résistantes au broutement, consommant plutôt des espèces riches en éléments nutritifs (Ritchie et al. 1998; Côté et al. 2004), et préférablement les individus de grande taille (Augustine & Frelich 1998; Knight 2003; Shelton et al. 2014). Par son broutement sélectif, le cerf de Virginie agit comme un filtre écologique en empêchant des espèces, pourtant bien adaptées aux conditions abiotiques du milieu, de persister dans le temps (Suzuki et al. 2013; Begley-Miller et al. 2014). Ce broutement sélectif peut ensuite induire un appauvrissement des communautés végétales touchées en favorisant la dominance d'espèces résistantes au broutement (fougères, graminoïdes, etc.) au détriment d'espèces sensibles (notamment, à fleurs et fruits développés) (Horsley et al. 2003; Rooney & Waller 2003; Suzuki et al. 2013; Begley-Miller et al. 2014). Ces dernières peuvent finalement être extirpées après des années de broutement intensif (Rooney & Dress 1997; Augustine & Frelich 1998; Knight et al. 2009). En fait, les effets du broutement intensif par les grands herbivores comme le cerf de Virginie peuvent persister au-delà de 20 ans après la réduction de leur effectif, créant des sous-bois appauvris, marqués par une difficile régénération forestière et une diminution de la diversité des angiospermes (Nuttle et al. 2013).

En raison de son broutement sélectif et de sa surabondance, le cerf peut induire une homogénéisation taxonomique des communautés végétales forestières (Rooney et al. 2004; Rooney 2009; Holmes & Webster 2011), soit une augmentation de la similarité dans la composition en espèces au sein d'un même site ou entre habitats (déclin de la diversité bêta) (McKinney & Lockwood 1999; Olden & Rooney 2006). Cette convergence des communautés vers un seul type d'assemblage, dominé par des espèces résistantes, non broutées ou généralistes (p. ex. exotiques, graminoïdes), peut aussi s'accompagner d'un déclin des espèces spécialistes (Rooney et al. 2004). À titre d'exemple, dans certaines forêts du nord-ouest de la Pennsylvanie, la surabondance de cerfs a éliminé la plupart des espèces de sous-bois, créant des parterres forestiers dominés par une seule espèce de fougère: *Dennstaedtia punctilobula* (Rooney 2001). Une telle communauté, dominée largement par une ou quelques espèces végétales remplissant des rôles fonctionnels similaires, ou encore marquée par la perte d'espèces ayant des rôles fonctionnels uniques, possède une faible diversité fonctionnelle (McKinney & Lockwood 1999; Olden & Rooney 2006; Clavel et al. 2011). Or, cette condition contribue à affaiblir la résistance et la résilience des communautés forestières face aux perturbations, en réduisant la diversité des

réponses possibles au sein des espèces touchées (Olden et al. 2004) ou même en altérant le fonctionnement et la productivité des écosystèmes (Clavel et al. 2011).

Enfin, les cerfs de Virginie peuvent simplifier la structure verticale d'un habitat forestier en induisant le déclin, voire l'extirpation, de strates sous-arborescentes (arbustes, gaules, semis) (McShea & Rappole 2000; Rooney 2001; Horsley et al. 2003). À plus long terme, l'élimination de ces strates peut induire des changements dans la composition et la structure de la canopée (Rooney & Waller 2003; Potvin et al. 2003; Long et al. 2007). Une étude portant sur l'impact du broutement sur la structure et la composition de forêts du parc national Manassas Battlefield (Virginie, É.-U.) a montré que la surabondance de cerfs de Virginie a contribué à extirper les semis de plusieurs espèces (p. ex. *Acer rubrum, Carya* spp.) après quatre ans de broutement intensif, au point d'influencer la composition future de la forêt vers une canopée dominée par des espèces résistantes au broutement (p. ex. *Prunus serotina, Celtis* spp.) (Rossell et al. 2005). La surabondance de cerfs de Virginie entraîne donc une cascade de conséquences pour l'ensemble du biote, allant d'un bouleversement de la flore de sous-bois à la modification de la structure et de la composition des peuplements forestiers.

1.1.2 Les espèces végétales introduites

Les espèces végétales introduites (synonyme: exotiques) sont des espèces absentes d'un milieu avant leur dissémination, volontaire ou accidentelle, par l'Homme (Richardson et al. 2000; Lavoie et al. 2012). Une forte proportion est dite naturalisée, c'est-à-dire que ces espèces peuvent s'établir et persister en nature sans assistance humaine (Richardson et al. 2000; Lavoie et al. 2012). Or, certaines de ces plantes naturalisées peuvent également devenir envahissantes, formant de vastes populations menaçant l'intégrité de la flore indigène (Richardson et al. 2000; Lavoie et al. 2012). Des espèces envahissantes reconnues pour être nuisibles dans les écosystèmes forestiers (p. ex. *Rhamnus cathartica*, *Alliaria petiolata*; Lavoie et al. 2014) ont d'ailleurs proliféré dans les zones agricoles et dans les boisés ceinturant le mont Saint-Bruno au cours des dernières décennies.

Les mécanismes favorisant les invasions floristiques sont néanmoins encore mal compris. Trois hypothèses ont été élaborées au cours des dernières décennies pour tenter une explication: (i) l'hypothèse de l'ennemi naturel, (ii) l'hypothèse de l'évolution compétitive et (iii) l'hypothèse des nouvelles armes biochimiques. La première suggère que le succès des plantes envahissantes repose sur la colonisation d'habitats libres de leurs compétiteurs spécifiques (p. ex. Maron & Vilà 2001; Levine et al. 2003), alors que la seconde soutient qu'en évoluant dans de tels habitats, sans

contrôle naturel, ces espèces peuvent allouer plus de ressources au développement d'avantages compétitifs (p. ex. Blossey & Nötzold 1995; Müller-Schärer et al. 2004). La troisième théorie stipule enfin que le succès de certaines plantes envahissantes serait lié à l'émission de composés chimiques (c.-à-d. allélopathie), entravant la croissance des autres plantes ou de la microfaune du sol des communautés envahies (Callaway & Ridenour 2004). Ces hypothèses font toutefois encore l'objet de débats. Les activités anthropiques, en altérant ou en détruisant carrément les habitats naturels, sont aussi d'importants vecteurs de propagation d'espèces exotiques, souvent pionnières et tolérantes aux perturbations (Grotkopp et al. 2002; Sutherland 2004).

Les forêts à canopée dense et fermée ont longtemps été considérées comme étant résistantes aux invasions floristiques (p. ex. Crawley 1987; Rejmánek 1989; Von Holle et al. 2003), puisque peu de plantes exotiques sont tolérantes à l'ombre (Sutherland 2004; Martin et al. 2009). Or, malgré leur nombre restreint, ces plantes forestières invasives pourraient causer d'importants préjudices à la flore indigène (Martin et al. 2009). Par exemple, le nerprun cathartique (*Rhamnus cathartica*), un arbuste très invasif (croissance rapide, graines nombreuses, fruits dispersés par les animaux, etc.) originaire d'Europe et d'Asie, forme de denses bosquets monospécifiques limitant la lumière au sol (Knight et al. 2007). Son feuillage, riche en azote, produit aussi une litière rapidement décomposée, ce qui contribue à exposer le sol et à en modifier le cycle de l'azote à l'avantage de ses propres semences (Heneghan et al. 2006; Knight et al. 2007). À terme, l'altération des conditions de sol et de lumière créée par cet arbuste généraliste favorise donc sa propre régénération au détriment de celle de la flore locale, appauvrissant de ce fait le cortège floristique des forêts envahies (Knight et al. 2007). Les forêts à canopée dense ne sont donc pas imperméables aux introductions d'espèces exotiques envahissantes, et les conséquences de ces introductions pour la flore indigène peuvent s'avérer majeures.

Les espèces exotiques sont d'ailleurs souvent associées au processus d'homogénéisation, délogeant la flore locale ou se répandant largement dans différents types d'habitats (McKinney & Lockwood 1999; Rooney et al. 2004; Qian & Ricklefs 2006; Lososová et al. 2012). L'introduction d'espèces peut donc favoriser une certaine modification des conditions abiotiques de l'habitat, voire même une homogénéisation biologique, et de ce fait, compromettre la résilience de la flore par la simplification du patrimoine génétique, des traits fonctionnels et de la diversité en espèces des communautés végétales envahies.

1.1.3 Verglas, sentiers pédestres et effets de bordure

Bien que les tempêtes de verglas soient courantes dans l'est de l'Amérique du Nord, faisant partie de la dynamique naturelle des forêts tempérées, l'ampleur et l'étendue de l'épisode de 1998 ont largement dépassé celles des tempêtes antérieures (Duguay et al. 2001). Cet épisode exceptionnel a ainsi induit une importante chute de branches dans les forêts touchées (Manion & Griffin 2001; Rhoads et al. 2002; Olthof et al. 2003), allant jusqu'à amputer une partie de la couronne des arbres (Brisson et al. 2001), si bien que de nombreux arbres n'ont pas complètement récupéré leur plein potentiel de croissance, même près de 10 ans après l'événement (Brisson et al. 2005). L'ouverture de la canopée par la création de trouées est une conséquence directe de cette altération de la couronne arborescente (Duguay et al. 2001; Darwin et al. 2004; Aarssen & Francq 2004; Beaudet et al. 2007). La taille de ces trouées est en général hautement variable, dépendamment de l'exposition à l'accumulation de glace, elle-même influencée par la topographie, la direction du vent, la tolérance des arbres touchés (Rebertus et al. 1997; Duguay et al. 2001; Bragg et al. 2003) de même que leur emplacement. Par exemple, certaines études portant sur l'effet du verglas ont rapporté que les arbres près des bordures et des milieux ouverts étaient particulièrement vulnérables à la chute de branches en raison d'une exposition accrue aux vents de tempête (Seischab et al. 1993; Päätalo et al. 1999). L'ampleur de la tempête de verglas de 1998 a justement contribué, dans certaines forêts, à créer de larges ouvertures, favorisant même un regain de lumière au sol (Aarssen & Francq 2004; Darwin et al. 2004; Beaudet et al. 2007), propice à l'établissement et à la croissance d'espèces indigènes (Aarssen & Francq 2004; Darwin et al. 2004; Beaudet et al. 2007) et exotiques (p. ex. *Rhamnus cathartica*; Darwin et al. 2004). Au parc national du Mont-Saint-Bruno toutefois, aucune évaluation précise des dommages n'a été réalisée suite à la tempête de verglas. L'équipe du parc suspecte néanmoins cette perturbation d'être à l'origine d'une baisse dans les effectifs de la phégoptère à hexagones (*Phegopteris hexagonoptera*) depuis 1999, une fougère rare associée aux forêts ombragées et non perturbées (Rivard 2012). Suite au verglas de 1998, certains peuplements matures ont en effet laissé place à une forêt en régénération, moins propice à l'espèce (Rivard 2012). Bien que certaines études aient démontré un retour rapide aux conditions de lumière au sol prévalant avant cet épisode historique de verglas (après 3-7 ans; Darwin et al. 2004; Beaudet et al. 2007), il est difficile de généraliser cette situation à l'ensemble des forêts touchées (p. ex. mont Saint-Bruno), étant donné la grande complexité des interactions topographie-composition-exposition. Le verglas, en contribuant à ouvrir la canopée, augmente néanmoins la présence de bordures au sein d'un habitat forestier, modifiant de ce fait les

conditions de lumière au sol durant quelques années après l'événement (durée proportionnelle à l'ampleur des trouées créées).

Les sentiers pédestres accentuent également la présence de bordures en forêt, en plus de faciliter le piétinement de la végétation adjacente (Wells et al. 2012; Barros et al. 2013), la compaction et l'érosion du sol (Kissling et al. 2009; Müllerová et al. 2011) et l'introduction de plantes exotiques (Baret & Strasberg 2005; Potito & Beatty 2005; Wells et al. 2012). Alors que le piétinement, la compaction et l'érosion du sol découlent directement de la construction et de l'utilisation des sentiers par les randonneurs (Barros et al. 2013), l'établissement de plantes exotiques en est une conséquence indirecte. L'effet de bordure associé à la présence de sentiers crée des conditions de lumière favorables à la germination d'espèces exotiques, qui persisteront si l'ouverture de la canopée est suffisamment importante (Baret & Strasberg 2005). Le piétinement et la dégradation des conditions édaphiques (compaction, etc.) en bordure des sentiers peuvent aussi favoriser les espèces exotiques, plus résistantes aux perturbations que les espèces indigènes (Lajeunesse et al. 1997; Grotkopp et al. 2002; Sutherland 2004; Potito & Beatty 2005). Les sentiers de randonnée agissent enfin comme corridor de dispersion pour ces plantes exotiques (Potito & Beatty 2005; Wells et al. 2012), ces dernières voyageant accrochées aux randonneurs (Mount & Pickering 2009). Ces impacts sont davantage marqués lors de la construction de routes, plus larges que les sentiers pédestres, contribuant parfois à transformer un habitat forestier continu en de petites zones d'habitat de bordure (Reed et al. 1996). Au parc national du Mont-Saint-Bruno, une route et plusieurs kilomètres de sentiers sillonnent la colline, donnant accès à presque l'entièreté des habitats forestiers. Des sentiers informels s'ajoutent aussi à ce réseau balisé, en plus des ravages de cerfs de Virginie. Ces circuits, additionnés à la création de trouées lors du verglas de 1998, sont donc autant de bordures et de voies de dissémination pour les espèces exotiques à travers ce territoire protégé.

1.2 La biodiversité en zones périurbaines: des interactions complexes et méconnues

Si l'urbanisation est reconnue comme étant l'un des principaux moteurs d'extinction d'espèces indigènes (DeCandido 2004; McKinney 2006; Schwartz et al. 2006), la situation de la biodiversité à la périphérie des agglomérations urbaines est moins claire (McKinney 2002, 2006). Plusieurs études ont en effet démontré que la flore des banlieues était parfois plus diversifiée que celle des zones rurales avoisinantes (p. ex. Kowarik 1995; Cornelis & Hermy 2004; Ranta & Viljanen 2011), en raison de l'hétérogénéité des paysages suburbains (McKinney 2002, 2006; Cornelis &

Hermy 2004; Ranta & Viljanen 2011). Des fragments d'habitats naturels y côtoient des milieux anthropisés (haies, jardins privés, friches, etc.), dont tirent profit certaines plantes généralistes urbanophiles (McKinney 2006). La flore suburbaine compte d'ailleurs de nombreuses espèces pionnières, tant indigènes qu'exotiques (McKinney 2006; Wittig & Becker 2010), ces dernières étant souvent dispersées par l'Homme (McKinney 2006). L'action de ces espèces sur la flore indigène des banlieues est toutefois encore méconnue. En ville, elles peuvent notamment contribuer à homogénéiser la flore locale en remplaçant certaines espèces (McKinney 2002, 2006; Schwartz et al. 2006; Wittig & Becker 2010) ou, à l'inverse, différencier les assemblages locaux selon la préférence des espèces exotiques pour les habitats présents et le moment de leur introduction (Kühn & Klotz 2006; Qian & Ricklefs 2006). Or, ces deux processus sont très peu documentés en zones périurbaines (McKinney 2006).

L'efficacité des aires protégées dans ces zones est tout aussi méconnue, alors que très peu d'études ont cherché à documenter l'état de la flore dans les parcs périurbains (Cornelis & Hermy 2004; Ranta & Viljanen 2011). Ces études ont, en outre, examiné la diversité floristique de ces aires protégées de manière ponctuelle, sans perspective historique. Pourtant, l'importance écologique des espaces verts urbains et périphériques, considérés comme étant d'importants refuges pour la faune et la flore locales (Goddard et al. 2009), souligne l'urgence de mieux documenter l'évolution de leur biodiversité, afin d'en assurer la pérennité en dépit des multiples perturbations associées au contexte d'urbanité (étalement urbain, espèces invasives, isolement au sein d'une matrice fragmentée, etc.). Au Québec, seules deux études historiques ont été conduites dans des parcs nationaux afin d'en évaluer l'efficacité (Lavoie & Saint-Louis 2008; Bourdages & Lavoie 2011). Or, ces études ont été réalisées en zones rurales; la méconnaissance de l'état de la diversité végétale en zone périurbaine demeure donc entière.

1.3 Des études historiques pour comprendre le présent

Les études de type archives historiques, ou «legacy studies», visent à mesurer les changements survenus au sein de communautés végétales à travers les ans, en comparant les résultats d'inventaires passés à ceux d'inventaires actualisés grâce à des ré-échantillonnages (Vellend et al. 2013). Une telle perspective temporelle permet d'évaluer, sur plusieurs décennies, la réponse des communautés végétales face aux variations de leur environnement (p. ex. Rogers et al. 2008; Damschen et al. 2010; McCune & Vellend 2013; Li & Waller 2015).

Le défi central des études historiques consiste à isoler le principal moteur des changements observés. Des inférences causales peuvent notamment être faites sur la base de la fluctuation de traits fonctionnels au sein des communautés étudiées (Wiegmann & Waller 2006; McCune & Vellend 2013). Par exemple, Li et Waller (2015) ont confirmé l'influence de la suppression des feux sur la flore des pinèdes des Plaines de sables du Wisconsin en constatant la progression de plantes tolérantes à l'ombre dans cette région au cours des 50 dernières années. De la même manière, Wiegmann et Waller (2006) ont suggéré le cerf de Virginie comme principal moteur des changements observés dans la végétation du Wisconsin au cours des six dernières décennies, en raison de l'augmentation d'espèces résistantes ou tolérantes à l'herbivorie concomitante à la diminution d'espèces sensibles au broutement. Les données historiques offrent ainsi un aperçu à long terme des changements écologiques, mais les conclusions sur leurs causes sont souvent indirectes (Vellend et al. 2013). Les interactions entre les processus, agissant sur différentes échelles temporelles et spatiales, peuvent également contribuer à complexifier le portrait global. Néanmoins, les études historiques contribuent à accroître notre capacité à prédire la réponse des plantes aux perturbations futures, en assurant une meilleure compréhension des changements passés et présents (Vellend et al. 2013).

Une étude de type «legacy», soit un inventaire phytosociologique, a justement été effectuée en 1976-1977 sur le mont Saint-Bruno (Gratton 1980). La qualité et la fiabilité de ces données anciennes ont d'ailleurs permis d'utiliser cette étude comme de point de départ pour étudier et documenter les changements floristiques survenus sur cette colline montérégienne au cours des 35 dernières années.

1.4 Objectifs de l'étude

L'objectif général de cette étude est de documenter la capacité d'un petit parc en région périurbaine à préserver l'intégrité de sa flore forestière, c'est-à-dire à la prémunir contre l'introduction d'espèces exotiques envahissantes ou la perte d'espèces spécialistes ou typiques de la flore des Montérégiennes (Raymond 1950), en dépit de fortes pressions anthropiques et de perturbations naturelles passées.

Les objectifs spécifiques du mémoire sont de :

1) Déterminer si la diversité de la flore forestière du parc national du Mont-Saint-Bruno a subi des changements en termes de richesse, de composition et de structure depuis 1977.

2) Déterminer si la flore forestière a subi une homogénéisation taxonomique et fonctionnelle depuis 1977.
3) Déterminer les facteurs possiblement à l'origine des changements observés.
4) Déterminer si les herbiers botaniques constituent une alternative crédible aux méthodes conventionnelles pour documenter l'impact du broutement du cerf sur la flore forestière.

Les résultats obtenus permettront d'évaluer l'efficacité réelle d'un petit parc sous pression à conserver et pérenniser la flore locale, en plus de proposer des recommandations pour maintenir ou renforcer les efforts de conservation.

1.5 Organisation du mémoire

Le corps du mémoire est constitué de quatre chapitres, dont deux rédigés sous forme d'articles scientifiques. Le premier chapitre présente une revue de littérature et une mise en contexte. Le second chapitre présente la reconstitution de la dynamique récente (35 ans) de la flore forestière du parc national du Mont-Saint-Bruno. Le troisième chapitre présente l'intérêt d'une nouvelle méthode basée sur des herbiers botaniques pour évaluer l'impact du broutement du cerf de Virginie sur la morphologie de plantes broutées. Enfin, le quatrième chapitre présente une conclusion générale au mémoire.

Le chapitre 2 sera soumis pour publication dans *Biological Conservation* tandis que le chapitre 3 sera soumis pour publication dans *American Journal of Botany*. Les auteurs sont Marie-Pierre Beauvais, Stéphanie Pellerin et Claude Lavoie. Le premier auteur a effectué l'échantillonnage sur le terrain, le traitement et l'analyse des données, ainsi que la rédaction du présent mémoire. Stéphanie Pellerin a supervisé le projet de recherche, en plus de corriger et de commenter les manuscrits. Claude Lavoie a également corrigé et commenté les manuscrits.

Chapitre 2: 35 years of vegetation change in a suburban park revealed no loss of functional diversity despite a significant convergence in species composition

2.1 Introduction

Biotic homogenization is the process by which local species invasions and extinctions reduce the variation of species composition across space (beta diversity) over time (Olden and Rooney 2006). The study of this process implies not only examining shifts in diversity but also the species gained and lost, as both exotic and generalist native species can promote homogenization by replacing specialist species (McKinney and Lockwood, 1999; Olden and Poff, 2003; Rooney et al., 2004). Furthermore, ecosystems subjected to a homogenization process may loss functional distinctiveness, with the establishment of species that fill similar functional roles in the community or with the loss of species that have unique roles (McKinney and Lockwood 1999; Olden and Rooney 2006; Clavel et al. 2011). It has been argued that the loss of functional diversity could ultimately weaken ecosystem resistance or resilience to disruptive events (Olden et al. 2004), or reduce ecosystem goods and services provided (Clavel et al. 2011).

Ecosystems located in an urban matrix are likely to experience greater homogenization than those located in a rural environment (McKinney 2006), since habitat alteration and fragmentation often put native species at a competitive disadvantage with exotic and generalist species (Byers 2002; McKinney 2006; Devictor et al. 2008). The extent to which suburban ecosystems, which share environmental characteristics with both urban and rural ecosystems, are homogenizing remains unclear (McKinney 2006). According to the intermediate disturbance hypothesis (Grime 1973; Connell 1978), suburban ecosystems should harbor higher floristic diversity than urban or rural ones due to the presence of more heterogeneous habitats (fragments of native vegetation, gardens, plantations, hedges, etc.) inside and surroundings their boundaries (McKinney 2002, 2006; Cornelis and Hermy 2004; Ranta and Viljanen 2011). Suburban ecosystems are thus likely to be characterized by a mix of native and exotic species (McKinney 2002, 2006; Ranta and Viljanen 2011) with a large array of functional traits. However, biotic homogenization may be unnoticed in those ecosystems, because beta diversity can be lost even though local and regional diversity remain unchanged or increase (Olden and Poff 2003; Van Calster et al. 2007; McCune and Vellend 2013; Li and Waller 2015).

In northeastern North America, suburban ecosystems, and mostly forests, must not only cope with anthropogenic disturbances associated with urban sprawl, but also with unprecedented densities of white-tailed deer (*Odocoileus virginianus*) populations (Cambrone 2013). Strict hunting regulations, reduction of natural predators, and increased high-quality forage supply caused by habitat modifications such as agriculture and land abandonment are the main factors associated with these dense deer populations (Côté et al. 2004), which often find refuge and food sources in suburban forests (Piccolo et al. 2010). White-tailed deer overabundance has been shown to be an important driver of plant community changes in temperate forests through selective browsing (Côté et al. 2004; Rooney 2009; Holmes and Webster 2011). By consuming palatable and nutrient-rich species (Ritchie et al. 1998; Côté et al. 2004), white-tailed deer act as a biotic filter (Begley-Miller et al. 2014), causing the disappearance of preferred species and the dominance of avoided or browsed-resilient ones (Horsley et al. 2003; Webster et al. 2005; Rooney 2009; Holmes and Webster 2011; Begley-Miller et al. 2014). Overbrowsing may therefore lead to a reduction in plant forest diversity (Rooney et al. 2004; Martin et al. 2010; Nuttle et al. 2013), plant population extirpations (Rooney and Dress 1997), and ultimately taxonomic and functional homogenization of forest stands (Rooney 2009; Holmes and Webster 2011).

Suburban natural parks may soon represent an extremely important conservation tool in a context where 54% of the world population now live in urban areas, a proportion expected to rise to 66% by 2050 (United Nations 2014). The current scarcity of empirical evidence of the effectiveness of parks for protecting wildlife, and especially plants, in suburban settings is therefore worrying. Protected areas are essential to safeguard species against extinction drivers (Cantú-Salazar and Gaston 2010), but several concerns have been raised about their capacity to achieve conservation objectives over decades (Terborgh 2004; Craigie et al. 2010; Laurance et al. 2012). This is particularly true for parks that have progressively been isolated within an urban matrix (Drayton and Primack 1996; Turner et al. 1996; DeCandido 2004). For example, DeCandido (2004) documented the extirpation of 25% of the native flora of Pelham Bay Park (309 ha; New York City) between 1947 and 1998, whereas the number of exotic species increased by about 40% over the same period due to growing human activities.

In this study, we investigated the floristic and diversity changes that occurred over a period of 35 years in the forest stands of a suburban park located in a major metropolitan region of North America. We revisited 133 plots originally surveyed in 1977 (Fig. 1). At that time, the park had not yet been created, but hiking activities were already well developed in the area due to a long

history of human influence. As the park was already isolated in an agricultural and suburban matrix, little habitat losses occurred in the surroundings over the last 35 years. However, since the 1977 survey, the number of visitors greatly increased, large population expansion of invasive species occurred in cultivated areas (i.e., *Anthriscus sylvestris*, *Rhamnus cathartica*, etc.), a major ice storm stroked the region and the deer population became overabundant. This study constitutes a first step toward a thorough documentation of suburban parks efficacy for preserving plant diversity over decades despite increasing disturbances. More precisely, we hypothesized that local species diversity (plot level) and regional diversity (park level) have increased due to the spread of generalist native and exotic species, favored by deer overbrowsing and hiking activities. On the other hand, we predicted that the number and abundance of specialist native plant and deer-preferred species decreased during the last decades, which resulted in a shift in community composition toward disturbance-resistant species. We also predicted that shade-intolerant species increased due to canopy gaps created by the ice storm and the creation of trails. All those changes resulted in the taxonomic and functional homogenization of the park.

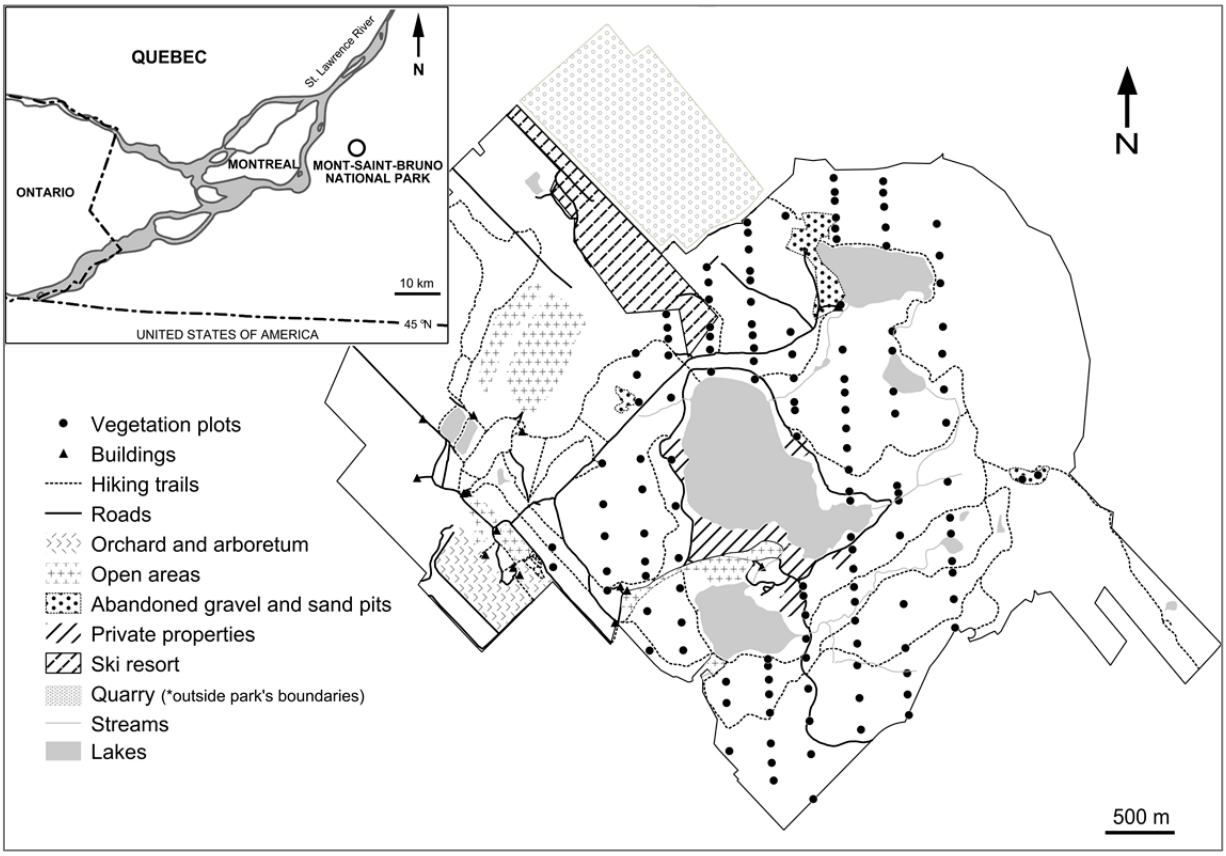

Figure 1. Localization of the Mont-Saint-Bruno National Park in southern Québec, Canada.

2.2 Methods

2.2.1 Study area

The study was conducted at Mont-Saint-Bruno National Park (hereafter: MSB; Fig. 1), a protected area of 9 km^2 established in 1985 near the city of Montréal in southern Québec, Canada (45° 32′ N; 73° 19′ W). The regional climate is humid continental with a mean annual temperature of 6 °C and a mean annual precipitation of about 1000 mm, 21% of which fall as snow (Environment Canada 2015). The Mount Saint-Bruno (maximum elevation: 218 m a.s.l) is one of the nine Monteregian Hills of the St. Lawrence Lowlands. The mountain is covered with deciduous forests dominated by *Acer saccharum* and *Carya cordiformis* at mesic sites at the base of the mountain, and by *Quercus rubra* or *Tsuga canadensis* on the thin and well-drained soils of the upper slopes. The hydrological network comprises several brooks, supplying five lakes and a small peatland. About 570 vascular plant species have been found in MSB (Gratton 1980), which represents almost 24% of the flora of the Québec province (Brouillet et al. 2015).

MSB ensures the protection of one of the few remaining large forests of the Montréal metropolitan region, the second most populous area in Canada with about 3.8 million inhabitants (Statistics Canada 2011). Due to its location within a densely populated region, MSB attracts about 880,000 visitors per year. The park foothills are surrounded by residential developments (mostly single-family houses), agricultural lands, a quarry (operated intermittently since 1928) and a ski resort (constructed in 1965). The park historical heritage is still visible in the landscape (e.g., water mills, orchard, arboretum, abandoned gravel and sand pits). Nine centennial private properties, covering about 10 ha, are present inside MSB boundaries near the largest lake, as are 30 km of hiking trails that provide access to most sectors of the park. About 60 ha of forest in the northern part of MSB were cut prior to 1940 (White et al. 2011). During the same period, selective cuts were practiced in some areas of the hill (near lakes and private houses). Nevertheless, beyond an altitude of 100 meters, over 70% of the forest remained undisturbed by human activities (Gratton 1980). Forest stands are mostly between 70 and 100 years (Québec 2008).

Two natural disturbances likely had a major influence on the MSB forest over the last decades. In January 1998, an ice storm, extreme in intensity and scale (Pellikka et al. 2000; Hooper et al. 2001), severely affected the entire region. No survey of the damage caused by the storm was conducted in the park, but some felling events were subsequently detected along the trails over a six-month period and extensive tree pruning were conducted over the same period

(MSB, pers. comm.). The second factor is the overabundant white-tailed deer population. While deer have probably always been a component of the park wildlife, the population reached a density of 8 deer/km^2 in the early 2000s (MSB, pers. comm.), which exceeds the carrying capacity (i.e., the number of deer that a given amount of land can support sustainably) of temperate forest ecosystems, estimated at 5 deer per km^2 (Huot and Lebel 2012).

2.2.2 Original plant survey: 1977

The forest vegetation of MSB was first surveyed in 1977 using 133 plots of 100 m^2 (Gratton 1980). The original sampling design avoided human-disturbed areas (old quarries, cutover and cultivated areas) and comprised 11 north-south oriented transects spaced by about 200 m. Plots along each transect were, on average, spaced by about 100 m. Each plot was set up in an area that appeared to be homogeneous in terms of plant composition. The cover (%) of all vascular plant species (used as a proxy for abundance) in each vegetation strata (herbs and forbs, shrubs, tree seedlings, tree saplings and mature trees) was estimated according to the Braun-Blanquet scale (Braun-Blanquet 1964). Habitat variables available in the original survey included: elevation, slope steepness and azimuth, plot position along the slope, stoniness and drainage.

2.2.3 Resampling: 2013

Sampling plots of 1977 were not permanently marked, but their respective location was precisely indicated on a map of MSB (1:6250). A hard copy of this map was digitized and georeferenced into Quantum GIS 2.0.4 software (QGIS, Open Source Geospatial Foundation Project, Beaverton, OR, USA), and the geographic coordinates of each plot retrieved. During the summer of 2013, the 133 original plots were relocated in the field using a global positioning system. In addition to geographic coordinates, all information available (habitat variables and general tree composition) from the original study was used to relocate the position of the plots as precisely as possible. Considering the abundance of human and natural markers (trails, houses, lakes, etc.) in the study area, we estimated that all the 1977 plots were relocated in 2013 within <25 m from their original position. When tree composition and habitat variables are used in combination with geographic location to relocate unmarked plots, relocation errors usually do not induce substantial biases when plant surveys are compared (McCune and Vellend, 2013; Kopecký and Macek, 2015).

The vegetation was resurveyed following the same methodology used in 1977. All plots were revisited from May to August using the same timeline as Gratton (1980), except for plots

initially surveyed in September and October, which were resampled in August. Habitat variables were not resampled, as they were assumed stable over time and used to relocate the plots.

2.2.4 Forest opening and edge effects

To evaluate the impact of forest opening and edge effects on the observed changes, we firstly estimated canopy openness (%) on the field by averaging four readings, one from each corner of the sampling plot, on a Lemmon's model C spherical densitometer (Lemmon 1956). This estimate was used to determine whether changes were greater in locally more open sites. Using a geographic information system produced by the MSB, we then measured the distance between each plot and the nearest open areas (e.g., lakes, recreational grounds and old fields, residential areas, unpaved roads and hiking trails) as an index of internal edge effects. Hiking trails (m per ha) within a radius of 100 m from the plots was also calculated as an index of hiking intensity.

2.2.5 Plant functional traits

A series of traits (Table 1) was compiled for all the species identified during the 1977 and 2013 plant surveys. Trait selection was based on the most likely drivers of changes at MSB (Appendix A), i.e., edge effect, ice storm, deer grazing and natural forest succession. Trait values (Appendix B) were gathered from the TOPIC database (Traits of Plants in Canada; Aubin et al. 2012) and from a literature review. The tolerance to disturbance of each species was estimated using their coefficient of conservatism (CC; Herman et al. 2001). The CC scores range from 0 (invasive or exotic species, species that can tolerate a wide range of environmental conditions and disturbances) to 10 (rare species or species with specific habitat requirements that do not tolerate disturbances). Although not a functional trait, each species was also characterized according to its origin (native or exotic; data from Lavoie et al. 2012, updated in Lavoie et al. 2014).

Table 1. Description of functional traits of plant species found in the forest of the Mont-Saint-Bruno National Park and used in the trait indicator and functional diversity analyses.

Trait	Code	Variable type	Classes and units
Morphological traits and life cycles and forms			
Maximum height	MH	Ordinal	1. <30 cm, 2. 31–100 cm, 3. 101–300 cm, 4. 301–500 cm, 5. >500 cm
Rhizome	RH	Binary	0. absence, 1. presence
Storage organ	ST	Binary	0. absence, 1. presence
Life cycle	LC	Ordinal	1. annual, 2. biannual, 3. perennial
Life form:			
Grass or sedge	GS	Binary	0. absence, 1. presence
Fern	FE	Binary	0. absence, 1. presence
Forb	FO	Binary	0. absence, 1. presence
Vine	VI	Binary	0. absence, 1. presence
Shrub	SH	Binary	0. absence, 1. presence
Reproduction traits			
Vegetative propagation	VP	Binary	0. absence, 1. presence
Seed dispersal vector :			
Abiotic	AD	Binary	0. absence, 1. presence
Biotic	BD	Binary	0. absence, 1. presence
Dispersal modes	DS	Ordinal	0. unassisted dispersal, 1. one mode, 2. two modes, 3. three modes, 4. >3 modes
Resource use trait			
Light requirement	LR	Ordinal	1. intolerant, 2. mid-tolerant, 3. shade-tolerant
Status	SS	Binary	1. native, 2. exotic
Disturbance and habitat quality traits			
Tolerance to disturbance	TD	Ordinal	1. CC: 0–3, 2. CC: 4–6, 3. CC: 7–10
Palatability	PA	Ordinal	1. avoided or rarely browsed, 2. moderately or occasionally browsed, 3. preferred or often browsed

2.2.6 Statistical analyses

Prior to analyses, species nomenclature was standardized in agreement with the VASCAN database (Brouillet et al. 2015). Plants identified in 1977 were checked using the herbarium specimens collected during this survey and now stored at the Université de Montréal Herbarium (MT). All specimens for which the identification was doubtful, or for which the absence of inflorescence impede the identification at the species level, were lumped into supra-specific ranks (e.g., *Carex*, *Poaceae*). Plants were classified in tree or understorey (grasses, sedges, forbs, ferns and shrubs) species subgroups, and analysed separately. The Braun-Blanquet cover classes were recoded using the van der Maarel 9-point scale (van der Maarel 1979) to better express differences in species dominance.

2.2.6.1 Changes in forest structure

Since a forest ecosystem is essentially structured by the different vegetation layers composed of tree species, the first step of our historical reconstruction was to verify whether there were cover changes (by species) in each of the layers considered (canopy, sapling and seedling). For this analysis, the cover data were transformed into percentages using the midpoint of each Braun-Blanquet class. Only species with >5% of mean cover for at least one of the sampling periods were used. Significant changes (2013 vs. 1977) were determined by Wilcoxon signed-rank tests. Species with the greatest changes in term of frequency of occurrence in each tree layers were also identified by comparing the proportion of the plots occupied by each species for each year using Chi-square goodness-of-fit tests.

2.2.6.2 Changes in understorey species richness and composition

To test the hypothesis that local and regional diversity have increased at MSB, changes in understorey species richness at the plot level between 1977 and 2013 were evaluated by Wilcoxon signed-rank tests. To assess differences at the park level, we rather estimated the total species richness of both years using the non-parametric First-order Jackknife estimator (Heltshe and Forrester 1983; Puhl et al. 2014) and evaluated significant difference using 95% confidence intervals (no overlap between the mean score of one group and the interval of the other; da Silva Monteiro et al. 2015).

Species that were significantly more frequent and abundant in 1977 or 2013 were identified with an indicator species analysis (ISA; Dufrene and Legendre 1997). Year was used as

partitioning criterion. The P-values were calculated with 9999 permutations and corrected with the Holm's method (Legendre and Legendre 2012). Significant indicator species of 2013 were then classified as 'winners', significant indicators species of 1977 were classified as 'losers', and the others as no change in accordance with McCune and Vellend (2013). To ensure biological and statistical significance, the analysis was restricted to species present in ≥10 plots sampled in at least one of the two sampling years.

A beta diversity partitioning analysis (Legendre 2014) was conducted to evaluate which processes were implied in the variation of the understorey species composition at the plot level over time (i.e., replacement of species by others, or species gain or loss). This analysis decomposes dissimilarities (D) between all pairs of plots (1977 vs. 2013) into two ecological processes, the species replacement (turnover) and the richness/abundance difference (species gain and loss, calculated for presence-absence or abundance data), in addition to calculate a similarity index (S = 1–D). As this study was carried out in a relatively small area, and that species composition should differ mostly in the abundances of the species, this analysis was performed with the percentage difference dissimilarity coefficient (*alias* Bray-Curtis dissimilarity coefficient) and using the 'beta.div.comp' function (Legendre 2014).

2.2.6.3 Biotic homogenization in the understorey flora

To test the hypothesis that a biotic homogenization occurred in the understorey flora of MSB, the total beta diversity (BD_{total} statistics) was first calculated for each site-by-species matrix (1977 and 2013), using the 'beta.div' function developed by Legendre and De Cáceres (2013). This function computes the total sum-of-squares of the site-by-species matrix, and then an index of total variance of this matrix, considered as an estimate of beta diversity. The effect of time on the total variance of the two site-by-species matrixes was then tested by computing a partial distance-based redundancy analysis (partial db-RDA; Legendre and Anderson 1999), using sampling plots as covariate. The overall canonical relationships and the effect of year were validated by significance tests with 9999 permutations. For both analyses, the percentage difference dissimilarity measure was chosen because it takes species abundances into account, it circumvents the double-zero problem (by ignoring simultaneous absence of a species at two sites; Legendre and Legendre 2012) and it is recommended for testing biotic homogenization (McCune and Grace 2002; Olden and Rooney 2006). Square root of dissimilarities was also used to obtain Euclidean matrixes.

To determine whether a loss of functional diversity occurred, functional richness (FRic), functional evenness (FEve) and functional divergence (FDiv) were calculated as complementary and independent components of functional diversity of plant assemblages (Mason et al. 2005; Villéger et al. 2008; Mouchet et al. 2010). Functional dispersion (FDis; Laliberté and Legendre 2010), which measures the dispersion of species in trait space without being affected by species richness or outliers like FRic, was also calculated. As we included ordinal and binary trait variables, the distance-based framework developed by Laliberté and Legendre (2010) was implemented to compute these four functional diversity metrics. Thereafter, Wilcoxon signed-rank tests were used to compare the results (1977 vs. 2013).

2.2.6.4 Main drivers of vegetation changes

To identify the functional traits that were significantly better represented over time (higher frequency and abundance in 2013 due to an increase of plants sharing those traits), and assuming that such traits could help to identify the drivers of vegetation changes, indicator traits (ITA) for each sampling year were identified using the ISA method. Only species present in >5% of the plots for each sampling year were used. For each year, trait-by-species and species-by-site matrixes were built and combined to calculate a Community Weighted Mean matrix (CWM; Garnier et al. 2004). The two resulting CWM (1977 and 2013) were overlaid and subjected to the ISA with 9999 permutations, using year as partitioning criterion. The P-values were corrected with the Holm's method (Legendre and Legendre 2012).

Linear regression analyses were also conducted to examine the relationship between species replacement values and abundance difference values obtained in the beta diversity partitioning analysis (used as response variables) and the canopy openness of each plot, the distance to the nearest internal edge and the hiking trails density (used as explanatory variables). Prior to analyses, replacement values were normalized by a log-transformation.

All statistical tests were carried out in R version 3.0.2 (R Core Team, Vienna, Austria) using the *stats* package (R Core Team 2013) for Wilcoxon signed-rank, Chi-square goodness-of-fit and linear regression analyses, the *vegan* package (Oksanen et al. 2013) for the Jackknife estimator and partial db-RDA, the *labdsv* package (Roberts 2013) for ISA/ITA and the *FD* package (Laliberté and Legendre 2010; Laliberté and Shipley 2011) for functional diversity indices and CWM.

2.3 Results

2.3.1 Changes in forest structure

No tree species significantly decreased in cover, in any layer, over the last 35 years (Fig. 2). The cover of three species in the canopy layer and of four species in the sapling layer significantly increased, and two species of the later (*Acer saccharum* and *Fagus grandifolia*) had a much greater cover in the sapling layer in 2013 than in 1977. No species in the seedling layer had significant cover changes.

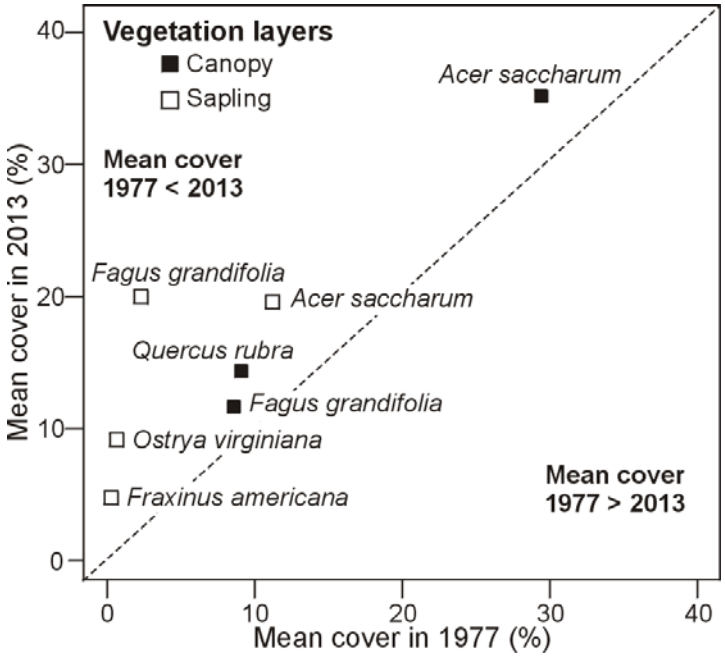

Figure 2. Mean cover of tree species of the Mont-Saint-Bruno National Park in 1977 vs 2013. Only species with significant changes within a specific vegetation layer are presented (Wilcoxon signed-rank tests; $P \leq 0.05$). The dashed line corresponds to no change.

Fagus grandifolia was the only tree species that was significantly more frequent in the canopy layer in 2013 compared to 1977 (Fig. 3), but plots with this species in their 2013 assemblages had small individuals (mean diameter at breast height: 21 cm; unpublished data), suggesting that they reached the canopy only recently. Seven species increased in frequency of occurrence in the seedling layer. Among them, *Fraxinus americana*, *Ostrya virginiana* and *F. grandifolia* also increased in the sapling layer. In contrast, only *A. saccharum* significantly decreased in frequency, but only in the seedling layer. Finally, *O. virginiana* and *F. grandifolia* were the only species that increased in cover and frequency of occurrence (Figs. 2 and 3).

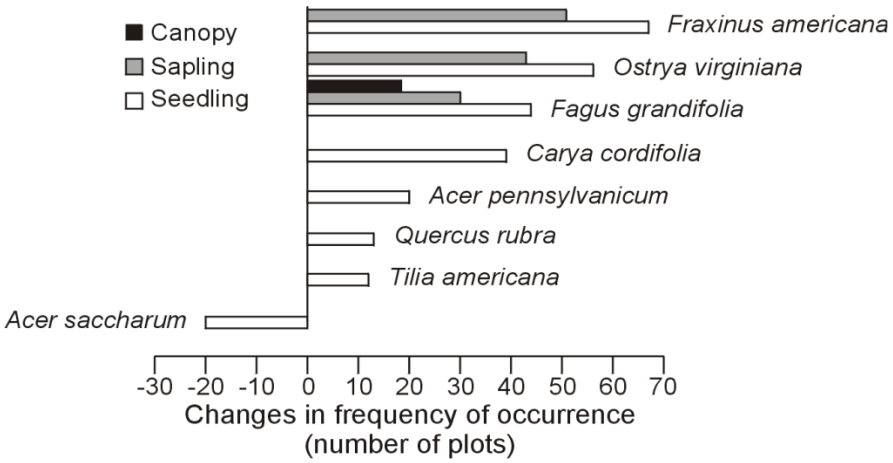

Figure 3. Significant changes (Chi-square goodness-of-fit tests; $P \leq 0.05$) in the frequency of occurrence (number of sampling plots) for the main tree species of the Mont-Saint-Bruno National Park in 1977 and 2013. Changes in frequencies were calculated by subtracting the number of plots occupied in 1977 from the number of plot occupied in 2013. Only species with significant changes within a specific vegetation layer are presented.

2.3.2 Changes in understorey species richness and composition

The diversity of understorey species at the park level significantly increased over time (Table 2). Forty-four new species (26 natives and 18 exotics) were detected in 2013, while 12 native species sampled in 1977 were not found in 2013. All species gained in 2013 were found in less than 10 plots, except *Panax quinquefolius* (10 plots), *Monotropa uniflora* (19 plots) and the exotic *Alliaria petiolata* (19 plots). Furthermore, they were all, except three exotics (*Rhamnus cathartica, Euonymus alatus* and *Coleus* sp.), previously recorded in 1976 in an exhaustive survey of plants growing in the open (field, roadside, wetland) or forest (outside the sampling plots) habitats of MSB (Gratton 1980). All species lost were present in less than three sampling plots in 1977.

Table 2. Total number of plants observed (γobs) and estimated (using the non-parametric First-order Jackknife estimator) in forest plots sampled in 1977 and 2013 from the Mont-Saint-Bruno National Park. Standard deviation (SD) and 95% confidence limits used to determine significant change in diversity over time are also indicated.

Year	γobs	Estimated values	SD	95% confidence limits
1977	100	133.7	7.8	118.4–149.1
2013	132	160.8	9.4	142.4–179.2

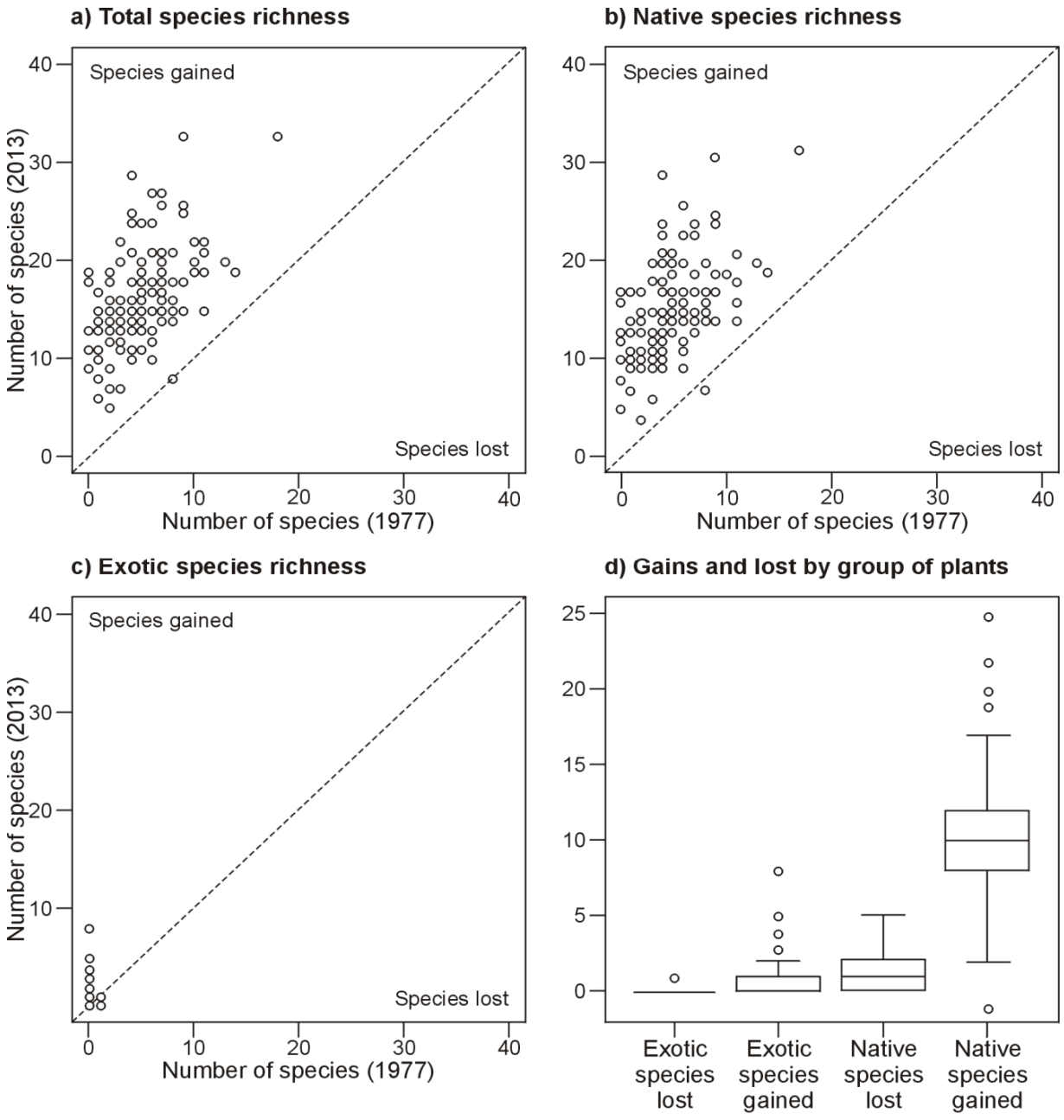

Figure 4. Species richness in the understorey of the forest of the Mont-Saint-Bruno National Park (plots sampled in 2013 compared to same plots sampled in 1977) for (a) all species, (b) native species and (c) exotic species. Boxplots (d) show the number of species gained and lost per vegetation plot. For each group of plants, the median (horizontal bar), 25 and 75 percentiles (box), 10 and 90 percentiles (error bars), and outlier values (circles) are indicated.

Table 3. Frequency (number of sampling plots) of the most frequent understorey plant species found in the Mont-Saint-Bruno National Park. Percentage of change between 1977 and 2013 are indicated only for species identified as "winners" by indicator species analysis ($P \leq 0.05$). Species are rank in order of frequency in 1977; respective rank in 2013 is also indicated.

Species	Freq. 1977	Freq. 2013	Change (%)	2013 Rank
Solidago caesia	49	113	+130	1
Polygonatum pubescens	45	111	+147	2
Thalictrum dioicum	42	86	+104	8
Uvularia sessilifolia	36	77	+114	10
Aralia nudicaulis	33	98	+197	4
Dirca palustris	31	51		16
Maianthemum canadense	30	96	+219	5
Maianthemum racemosum	29	64	+120	12
Trillium grandiflorum	28	91	+224	7
Oclemena acuminata	24	51		15
Poaceae spp.	24	95	+294	6
Uvularia grandifolia	17	32		20
Carex spp.	13	100	+675	3
Nabalus altissimus	12	71	+487	11
Epipactis helleborine	9	80	+785	9

Understorey species richness per plot tripled between 1977 and 2013 ($Z = 8778$, $P < 0.0001$; Fig. 4a). Native richness also significantly increased, from an average of 5 to 15 species per vegetation plot ($Z = 8910$, $P < 0.0001$; Fig. 4b), whereas the exotic richness only increased by an average of one species per plot ($Z = 3852$, $P < 0.0001$; Fig. 4c). Overall, each plot has gained more natives than exotics, and lost only one native (Fig. 4d). Of the 54 species present in ≥10 plots, 32 were identified as 'winners' and 22 as 'no change'; there was no 'loser' (Appendix C). Although the identification of several winner species, the most frequent species remain nearly the same between 1977 and 2013 (Table 3). 'Winners' were mostly perennial, shade-tolerant native forbs (Appendix C). Most were also mid-tolerant to disturbances (CC 4 to 6). Among the winners, palatable species (13) were as numerous as unpalatable ones (14).

According to the beta diversity partitioning analysis (Fig. 5), the among-time variation in the understorey species diversity was mainly associated with a difference in the species abundance, instead of a species replacement. As a result of the important species gain in 2013, the similarity in species composition among years remained low.

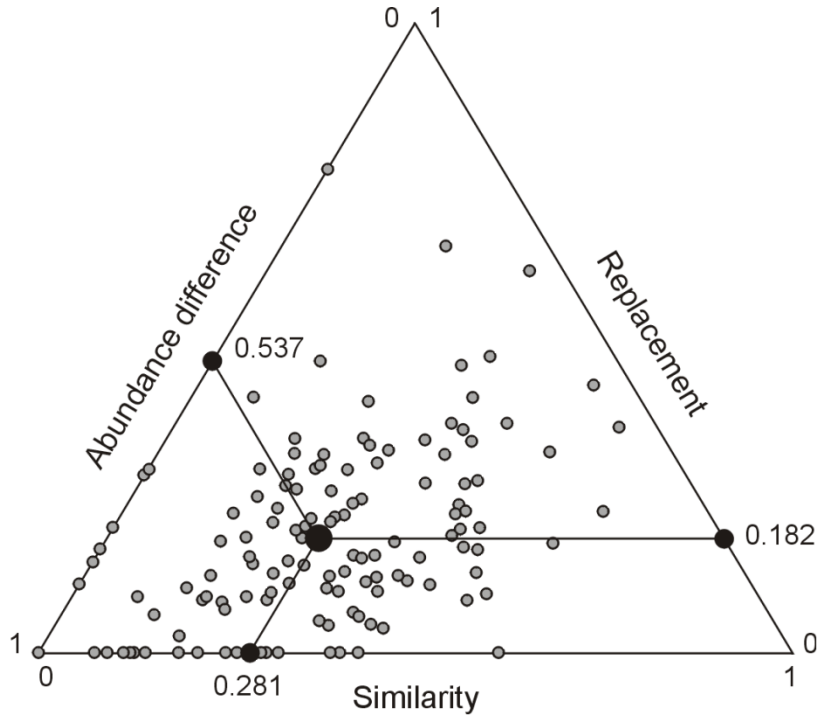

Figure 5. Relationships among the 133 pairs of sites (vegetation plots sampled in 2013 compared to same plots sampled in 1977) surveyed in the Mont-Saint-Bruno National Park. Each grey dot represents a pair of plots. Their position is determined by a triplet of values from the similarity, replacement and abundance difference matrices (see text for details). The large black dot is the centroid of all grey dots; the other black dots represent the mean value of the three components of beta diversity axes.

2.3.3 Biotic homogenization in the understorey flora

Total beta diversity of understorey plant species decreased by 30% from 1977 to 2013 (0.44 to 0.31; Fig. 6). Time had a small but significant effect on the total variance of both community matrixes (R^2_{adj} = 5.4%; P <0.0001), indicating a significant difference in the beta diversity over the last 35 years. Graphic representation of the 95% confidence ellipse for centroids also indicated that a biotic homogenization occurred in the MSB flora, as the ellipse was smaller in 2013 than in 1977, illustrating a convergence in species composition in 2013 (Fig. 6).

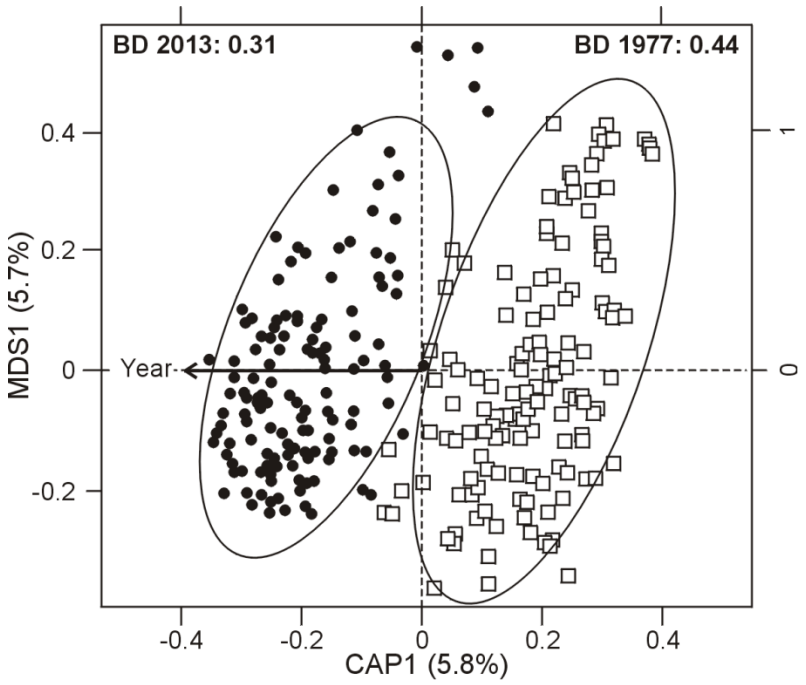

Figure 6. Results of time-constrained partial db-RDA of vegetation plots sampled in the Mont-Saint-Bruno National Park in 1977 and 2013. For each axis, the percentage of the variance explained is indicated. Year is the explanatory variable. White squares represent the 1977 plots, and black dots the 2013 plots. The 95% confidence ellipses for centroids for both sampling years are shown. BD is the beta diversity value for each.

However, the taxonomic homogenization observed did not result into a functional homogenization, as the values of FEve, FRic and FDis were significantly higher in 2013 than in 1977 (Table 4). In contrast, FDiv was significantly smaller in 2013 than in 1977.

Table 4. Functional evenness (FEve), functional divergence (FDiv), functional richness (FRic) and functional dispersion (FDis) values of the forest vegetation of the Mont-Saint-Bruno National Park in 1977 and 2013.

Diversity metric	1977	2013	Wilcoxon statistic (Z)	P
FEve	0.481	0.751	6698	<0.0001
FDiv	0.814	0.753	1973	<0.0001
FRic	0.235	0.348	4349	<0.0001
FDis	1.157	3.731	8253	<0.0001

2.3.4 Main drivers of temporal changes

According to the ITA, understorey plant species found in 2013 were more likely to have a storage organ (ITA = 0.65; P = 0.002), and to be a grass/sedge (ITA = 0.53; P = 0.002) or a fern (ITA = 0.33; P = 0.017). No indicator trait was significantly associated with the plants recorded in 1977.

No significant relationship was found between canopy openness and species replacement values (P = 0.23) or with abundance difference values (P = 0.55). Similar results was obtained between the distance to the nearest internal edge and species replacement values (P = 0.17) or with abundance difference values (P = 0.15) as well as between the hiking trails density and species replacement values (P = 0.06) or with abundance difference values (P = 0.12).

2.4 Discussion

In this study, we documented changes in the structure and composition of the forest stands of a suburban park over the past 35 years. We found that alpha (plot level) and gamma (park level) diversity greatly increased over time, essentially due to the spread of native species. This finding diverges from the general pattern of biodiversity loss usually associated with the increase of human influence on ecosystems (Barnosky et al. 2011; Pereira et al. 2012). It nevertheless concurs with recent works that demonstrated an increase in local diversity over time (Van Calster et al. 2007; Johnson et al. 2014; Puhl et al. 2014; Li and Waller 2015), even in human-disturbed landscapes (McCune and Vellend 2013). For instance, McCune and Vellend (2013) found a significant increase in local diversity over four decades in a highly urbanized area of southern Vancouver, driven by both native and exotic species. A recent meta-analysis also revealed no clear tendency for plant diversity changes at local scales, suggesting that community responses to environmental changes is context-dependent (Vellend et al. 2013). On the other hand, the observed increase in alpha and gamma diversity was accompanied by a decrease in beta diversity, meaning that a biotic homogenization occurred in the MSB forest stands, though no functional homogenization was detected.

2.4.1 Biotic and functional homogenization

As recently observed in some forests of North America (e.g., McCune and Vellend 2013; Li and Waller 2015), biotic homogenization in MSB was essentially associated to a gain in native species. In central sand plains (Wisconsin), Li and Waller (2015) found a strong pattern of species composition convergence since 1958 in pine barrens, mostly driven by an increase in canopy

coverage and shade-tolerant native species due to fire suppression. McCune and Vellend (2013) also attributed biotic homogenization in southern Vancouver to gain in natives rather than increase in exotic species, despite human disturbances. In our study, as in the two previous ones, homogenization reflected changes in natives rather than exotic species, since each plot gained on average only one exotic species over time, while the native species richness tripled since 1977. Temperate forests of eastern North America are usually considered to be resistant to invasions (Von Holle et al. 2003; Lavoie and Saint-Louis 2008) because most exotic plants of this region are shade-intolerant, predominantly early-successional species (Grotkopp et al. 2002; Sutherland 2004). Despite the pool of shade-tolerant plant invaders is relatively small, the long-term effects of invasions could potentially be severe (Martin et al. 2009). For instance, *Alliaria petiolata*, one of the two exotic 'winners' in MSB, is a shade-tolerant plant that has many competitive advantages that contribute to its status as an highly invasive species, e.g., a broad ecological niche, a prolific seed production, a large number of seed dispersal vectors, flowers adapted to generalist pollinators and an ability to self-pollinate (Cruden et al. 1996; Rodgers et al. 2008).

The taxonomic homogenization observed at MSB did not, however, lead to a loss in functional diversity (FD). Higher functional richness and dispersion in 2013 imply a greater dispersion of species in trait space, i.e., a larger range of trait values in the community (Villéger et al. 2008; Laliberté and Legendre 2010). These index are interpreted as an indicator for potentially used/unused trait space and thus for productivity (Mason et al. 2005). Higher values in 2013 then suggest a better use of habitat resources and a higher productivity of flora in 2013 than in 1977. A higher FRic in 2013 is consistent with the fact that among-time variation in the MSB flora diversity is related to species enrichment, thus promoting productivity, as FRic is positively correlated to species richness (Villéger et al. 2008). Functional evenness quantifies the regularity of the distribution of species in trait space, weighted by their abundance (Villéger et al. 2008). FEve is used to indicate under/over-utilization of resources, and again productivity. For instance, assuming a continuous resource availability throughout trait space, lower functional evenness indicates that some parts of the trait space are densely occupied while others are empty, and then, under-utilized (Mason et al. 2005). Higher FEve in 2013 thus likely means a more effective utilization of the resources available due to a more even distribution of abundance species in trait space. Finally, functional divergence calculates how species diverge from the center of gravity in the trait space (Villéger et al. 2008; Mouchet et al. 2010). Low levels of FDiv (as observed in 2013) thus suggest low degree of niche differentiation among species within communities: the

most abundant species are similar and firmly compete (Mason et al. 2005; Mouchet et al. 2010). Despite this lower niche differentiation, MSB flora is expected to be more resistant to disruptive events than in 1977 (Olden et al. 2004), according to its higher FD.

2.4.2 Canopy gaps and edge effects on forest structure and composition

Contrary to expectations, we found no evidence that the opening of the stands due to the 1998 ice storm or the trails development, and then edge effects, promote a shift in community composition toward disturbance-resistant and/or shade-intolerant species. Instead, we found a major increase in frequency and abundance of native shade-tolerant species, suggesting a general trend toward forest maturation due to the end of logging. Several studies on the response of forest understory vegetation to ice storms also revealed a brief modification of the understory light conditions due to a branch sprouting (Duguay et al. 2001; Brommit et al. 2004) or the development of a sub-canopy layer caused by the growth of released saplings (Brisson et al. 2001; Olthof et al. 2003; Darwin et al. 2004), and thus a rapid return to pre-ice storm conditions favoring shade-tolerant species (Darwin et al. 2004; Beaudet et al. 2007). As observed in those studies, the sub-canopy layer of the MSB forest stands showed an important increase in the sapling cover and abundance, creating a more heterogeneous forest structure. Canopy gaps, right after the 1998 ice storm, could have promoted the germination of tree seedlings and then, the densification of the sub-canopy layer over the years. *Fagus grandifolia* was also the only tree species that was significantly more frequent in the canopy layer in 2013 which is consistent with Rhoads et al. (2002) that documented an increase in small-diameter individuals of this species after the 1998 ice storm at the Hubbard Brook Experimental Forest (USA) due to its root sprouting potential. The absence of a significant decline in the cover of species in the tree layer further suggests that the ice storm has had no long term impact on the canopy. This canopy maturation has probably contributed to mitigate edge effects of trails, now undetectable as revealed by linear regression analyses.

2.4.3 Deer influence on understorey species composition

Overall, our results suggest that deer selective browsing had some influence on species composition of MSB forest stands, as ferns, sedges/grass and species with storage organ, commonly found in high deer density sites (Horsley et al. 2003; Rooney 2009; Frerker et al. 2013; Bachand et al. 2014), significantly increased in frequency and abundance over time. These species groups are resilient to browsing because of their rhizomes, basal meristems or below ground

reserves (Coughenour 1985; Frerker et al. 2013; Bachand et al. 2014). As a result, graminoid plants and species with storage organ (i.e., *Arisaema triphyllum* and *Nabalus altissima*) are now found in more than half of the plots, therefore contributing to taxonomic homogenization. Furthermore, despite some 'winner' species were palatable, we observed in the field that individuals (except for *Aralia nudicaulis*) were often small, under the browsable 'molar zone' (>10 cm; Dobson and Blossey 2015), without fruits or flowers (M.-P. Beauvais, personal observations). For example, *Trillium grandiflorum*, a deer-preferred species, was generally found in the small vegetative three-leaf stage, commonly observed in overbrowsed populations (Knight 2003; Knight et al. 2009). Its persistence despite intense browsing could be related to its long-lived nature and its particular demographic dynamic (Knight et al. 2009). Under intense browsing pressure, the persistence of native flora could thus be time dependent (Horsley et al. 2003; Kraft et al. 2004; Knight et al. 2009). This suggests that our diversity peak could be temporary, given most palatable MSB forest species have long-lived nature and an average tolerance to disturbance (CC 4 to 6) that allow them to persist, until continuous intense browsing could extirpate them.

2.5 Conclusion

Our findings highlight the crucial role of suburban parks in preserving native flora, despite natural and anthropogenic disturbances. Conservation efficiency of this suburban park against exotic invasion and biotic homogenization, although its small size, appears to be much higher than what is usually observed in urban parks (Drayton and Primack 1996; Turner et al. 1996; DeCandido 2004; McKinney 2006) and quite close to rural parks (Lavoie and Saint-Louis 2008; Bourdages and Lavoie 2011). As a result, 'winner' species included specialist forbs strongly associated with ancient forests (i.e., *Actaea rubra, Asarum canadense* and *Osmorhiza claytonia*; Hermy and Verheyen 2007) or indicator of habitat integrity (i.e., *Hieracium paniculatum* and *Panax quinquefolius*; CC 10). Furthermore, our results showed that no functional diversity loss occurred despite species convergence suggesting no community impoverishment. Restrictive conservation status, such as national park (IUCN Category II; International Union for Conservation of Nature 2015), may contribute to better manage visitor use (e.g., vegetation trampling, creation of narrow trails favoring a dense canopy, etc.) in suburban settings – where human pressure is acute – than in other green spaces. However, to maintain viable assemblages of native plant species, close monitoring and management of threats (e.g., invasive species) is required, as drivers of change in suburban areas are often multiple and interacting.

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Chapitre 3: Herbarium specimens contribute to confirm the dwarfing of *Trillium grandiflorum* in high deer density sites

3.1 Introduction

Over the last century, populations of large ungulates have greatly increased in many regions of the world due to strict hunting regulations, reduction of hunting pressure and natural predators, and increase of food supply associated with land use change (Côté et al. 2004). Overbrowsing by ungulate herbivores has often induced tremendous changes on forest composition and structure, and is consequently becoming a major conservation issue (Côté et al. 2004; Begley-Miller et al. 2014). For example, in temperate forests of northeastern North America, selective browsing by *Odocoileus virginianus* (White-tailed deer) has prevented the regeneration of many shrub and tree species (Hidding et al. 2012; Nuttle et al. 2013), and caused the local disappearance of preferred species and the dominance of avoided or browsing-resilient ones (Horsley et al. 2003; Webster et al. 2005; Begley-Miller et al. 2014).

Although the effect of overbrowsing on forest composition is relatively well known, the understanding of the long-term impact of intense deer herbivory on plant populations is more limited (Webster et al. 2005; Knight et al. 2008; Collard et al. 2010). Deer can directly threaten growth, reproduction and survival of plants by removing leaves, buds, shoots, flowers and fruits (Côté et al. 2004), but can also induce changes on plant fitness. For example, studies conducted on *Trillium grandiflorum* (White Trillium), a species largely consumed by deer in eastern North America, showed that repeated browsing reduces the proportion of flowering individuals and plant height over time (Anderson 1994; Augustine and Frelich 1998; Rooney and Waller 2001; Knight 2003; Knight et al. 2009). More specifically, intense and repeated deer browsing skews population structure toward smaller plants (Anderson 1994; Augustine and Frelich 1998), and consequently alters the reproductive success of individuals as small *Trillium grandiflorum* plants produce fewer ovules (Knight 2003). Over the long term, overbrowsing could potentially cause the local extinction of this species (Knight et al. 2009).

Having a spatial and historical perspective on the long-term impact of overbrowsing on plant fitness is a difficult task because forest vegetation is rarely monitored over more than a few years. On the other hand, plant specimens that have been collected for several decades and preserved in herbaria may provide the data needed for establishing such perspective (Lavoie 2013). Herbarium specimens have successfully been used in a few studies to document plant morphological changes (McGraw 2001; Law and Salick 2005; Guerin et al. 2012; Leger 2013). For instance, Law and

Salick (2005) showed, using museum collections and modern specimens, that sustained human harvesting over 100 years of a medicinal Tibetan plant (*Saussurea laniceps*) resulted in a size reduction of the species. Herbarium data also showed that large-scale harvesting of *Panax quinquefolius* in North America caused significant plant size decline since the beginning of the 20th century (McGraw 2001).

The potential of herbarium collections for reconstructing plant morphological changes opens new opportunities for documenting the spatiotemporal patterns of the impacts of natural and anthropogenic disturbances. However, this potential needs to be more thoroughly tested, especially because the use of herbarium specimens are subjected to several biases that have to be taken into account before concluding on the impacts (Delisle et al. 2003; Lavoie 2013). In this study, we used herbarium specimens to investigate the potential impact of overbrowsing by *Odocoileus virginianus* on the size of *Trillium grandiflorum* individuals from southern Québec (Canada). More precisely, we compared long-term trends in the size of herbarium individuals to those of modern specimens sampled in forests subjected to overgrazing by deer, and to sites without deer. Leaf area was used as an indicator of plant size, because this morphological trait is considered a reliable estimate of the plant size (Anderson 1994) and its reproductive potential (Knight 2003).

3.2 Methods

3.2.1 Study species

Trillium grandiflorum is a non-clonal, long-lived, perennial herb that grows in the understorey of deciduous forests throughout eastern North America (e.g., Case and Case 1997; Knight 2003). Reproductive plants are characterized by the presence of a single stem, rarely two, supporting a whorl of three leaves and one hermaphrodite white flower producing a single fruit (Knight 2003). Seeds are mainly dispersed by ants (Case and Case 1997; Kalisz et al. 1999). They produce small adventitious roots during the first year of growth, whereas the cotyledon emerges in the second year, and the first true leaf unfolds the third year (Hanzawa and Kalisz 1993; Knight et al. 2008). This species begins to reproduce after about 17 years, but an individual can become dormant for one or several years (Hanzawa and Kalisz 1993; Knight 2003). In southern Québec, most leaves appear late April, before the forest canopy leafs out. Flowering occurs from mid to late May.

Odocoileus virginianus consumes preferentially large reproductive *T. grandiflorum* plants (Anderson 1994; Knight 2003), and consumption usually results into a complete defoliation (Anderson 1994; Augustine and Frelich 1998; Knight 2003). Browsing stops growth, but few

individuals die after a single consumption event (Knight 2003; Rooney and Gross 2003), although browsed plants are more likely to retrogress to a vegetative stage the next spring (Knight 2003; Rooney and Gross 2003; Knight et al. 2009).

3.2.2 Herbarium specimen sampling

Herbarium specimens of *T. grandiflorum* sampled in Québec were requested from the four most important (>137,000 specimens) herbaria of the province (MT, MTMG, QFA, QUE), and from the two Canadian national herbaria (CAN, DAO), for a total of 794 specimens. Only specimens with fully opened flowers, with at least two undamaged leaves, and with precise sampling location and date were retained. Specimens collected after May 31th were also discarded, to only keep those with a similar growth period. Additional information recorded were specimen number, habitat characteristics and name of collectors. A leaf area index was calculated (width at the widest point multiplied by the length from the base to the tip) and averaged for each selected specimen (n = 692 specimens).

Leaf area of herbarium specimens can be influenced by the preference of collectors for the biggest or healthiest individuals, and by other factors like temperature and moisture (Peppe et al. 2011), which fluctuate in space and time. An increase of leaf area in the recent years may potentially be related to warming temperatures associated with climate change (Guerin et al. 2012). In order to track the climate signal over time, herbarium specimens were divided into two groups, i.e., collected <1971 and ≥1971; this threshold year corresponds to the year during which the growing season began to extend in southern Québec in spring time, from a few days to about two weeks, depending on the location (Zhang et al. 2011; Audet et al. 2012). Here, the beginning of the growing season in spring is defined as the moment of the year when the daily mean temperature is ≥5 °C for at least six consecutive days. A regional climate effect was also tested by grouping specimens according to their bioclimatic region, using the classification of Grandtner (1966): (1) *Acer saccharum – Carya cordiformis* region, (2) *Acer saccharum – Tilia americana* region, and (3) *Acer saccharum – Betula allegheniensis* region. In both cases (time and space), significant differences between groups would suggest that differences in leaf area are potentially climate-dependent. A site effect was also tested by grouping the specimens according to their location (Table 1), since most *T. grandiflorum* specimens (n = 597) were sampled in a relatively small number of locations of the *Acer saccharum – Carya cordiformis* bioclimatic region, either

on the Mount Royal Park (Montréal), in other sites of the Montréal Island, or on the Monteregian hills.

Table 1. Modern and herbarium *Trillium grandiflorum* specimens used to evaluate the impact of *Odocoileus virginianus* overbrowsing on their leaf area over time and space in southern Québec

Specimen types	Sampling years	n	Leaf area index mean ± SD (cm^2)	Deer density
Modern specimens				
Mont-Saint-Bruno National Park (MSB)	2013	489	43.8 ± 16.4	8 deer/km^2
	2014	202	37.5 ± 13.4	8 deer/km^2
Fernand-Séguin Ecological Center (FSEC)	2014	471	43.6 ± 11.3	5 deer/km^2
Mount Royal Park (MRP)	2014	350	74.1 ± 30.1	No deer
Montréal Botanical Garden (MBG)	2013	287	62.8 ± 25.2	No deer
	2014	265	68.3 ± 28.3	No deer
Herbarium specimens				
All specimens pooled	1848–2011	692	58.6 ± 36.5	–
A. saccharum – C. cordiformis region	1848–2011	597	57.8 ± 36.9	–
Montreal Island	1848–1997	213	54.6 ± 40.7	–
Monteregian hills others than Mount Royal	1920–2011	199	60.5 ± 33.4	–
Mount Royal Park (without bias; see text for details)	1874–1987	65	51.6 ± 29.0	–
Mount Royal Park (bias included; see text for details)	1874–1987	73	47.4 ± 33.7	–

3.2.3 Field sampling

The modern *T. grandiflorum* population with clear evidence of overgrazing (Fig. 1) that was used in this study was located in the Mont-Saint-Bruno National Park (MSB), a 900 ha park established in 1985 near Montréal (45°33'N; 73°19'W) to protect one of the nine Monteregian Hills of the St. Lawrence Lowlands. The Mount Saint-Bruno (maximum elevation: 218 m a.s.l) is covered by deciduous forests dominated by *Acer saccharum* and *Carya cordiformis* on mesic sites at the base of the hill, and by *Acer saccharum*, *Tsuga canadensis* and *Quercus rubra* on well-drained slopes with thin soils (Gratton 1980). The *O. virginianus* has been present in the park since at least the mid-1980s, but reached a density of approximately 8 individuals per km^2 in the early 2000s (MSB, pers. comm.). Populations of *T. grandiflorum* were scouted at MSB during the flowering period in 2013 and 2014 (9–15 May 2013; 14 May 2014). Only individuals visible from hiking trails were sampled; the hiking trail network is extensive (30-km long) and gives access to most park sectors.

The leaf area index of the leaves of each flowering individual was calculated as for herbarium specimens. Damages to the leaves were also noted.

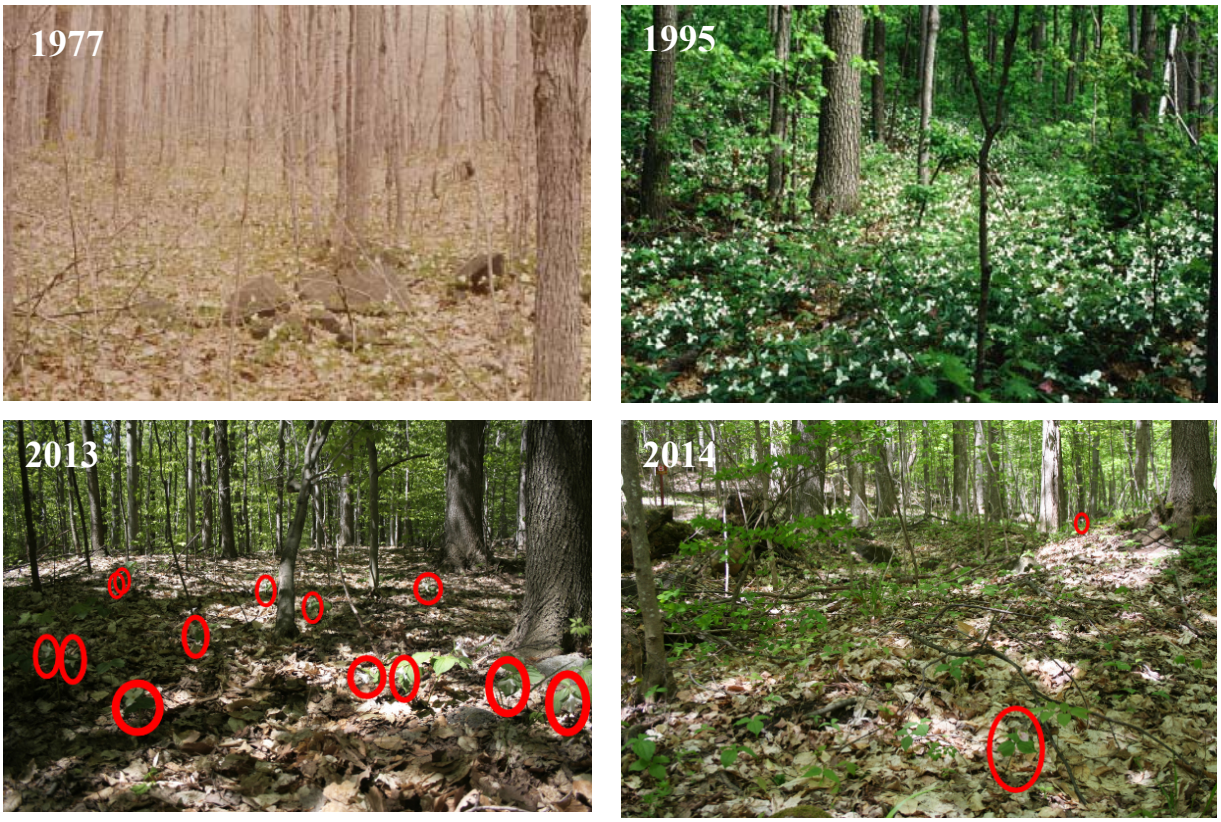

Figure 1. *Trillium grandiflorum* populations in the maple forests of Mont-Saint-Bruno National Park (Québec, Canada). In 2013 and 2014, only a few individuals with a flower remained (surrounded by a red circle). From left to right, top to bottom: 1977 (photograph: Louise Gratton), 1995 (Donald Rodrigue, MSB), 2013 and 2014 (Marie-Pierre Beauvais). Although the photographs were not taken at the same location, they were deemed representative of the overall situation by park wardens.

Other populations (with and without deer) were sampled for comparison purposes. The Fernand-Séguin Ecological Center (FSEC; 45°21'; 73°47'W), a 60 ha suburban park near Châteauguay (about 30 km from MSB), was potentially impacted by deer. According to the latest aerial surveys (1997, 2006 and 2008) in the vicinity of the park, deer density was about 5 individuals per km^2. However, in the Montréal region, deer density in forests is often greater than the estimated regional density since they are frequently used as refuges by the animals (Huot and Lebel 2012). FSEC is covered by an *Acer saccharum* and *Carya cordiformis* forest, and although deer are abundant, large populations of *T. grandiflorum* are still present. All flowering

individuals present in 20 circular quadrats (1 m^2) randomly located in the forest of FSEC were measured for leaf area (15 May 2014).

Natural forest sites with *T. grandiflorum* but without deer are rare in the Montréal area: the Mount Royal Park (MRP; 45°31'N; 73°36'W; 200 ha) and the Montréal Botanical Garden (MBG; 45°33'N; 73°33'W; 75 ha) are two of them. The MRP, located in the heart of the Island of Montréal, has the same geological origin as MSB (Monteregian hill; 233 m a.s.l.). Two MRP forest stands, both dominated by *Quercus rubra* and *Acer saccharum*, were sampled in 2014 (16 May). Two unmanaged forest stands in MBG, dominated by *Fraxinus pennsylvanica* and *Ulmus americana* or by *Acer saccharum*, were sampled in 2013 and 2014 (15 May 2013, 17 May 2014). All these stands were sampled the same way as at FSEC. It should be noted that according to the maps of urban heat islands created for the Montréal region (Centre d'enseignement et de recherche en foresterie de Sainte-Foy and the Institut national de la santé publique du Québec 2012), the surface temperature of these urban parks oscillates between 15.9 to 18.7 ºC, which is similar as that of MSB (15.9 to 17.6ºC).

3.2.4 Statistical analysis

Prior to analyses, data were log-transformed to normalize their distribution. A Welch's *t*-test was used to test for significant differences between herbarium specimens sampled <1971 and ≥1971, as the assumption of homogeneity of variances was not met and sample sizes were unbalanced. A one-way ANOVA, using type III sums of squares for unbalanced design, was used to test for significant differences between herbarium specimens from different bioclimatic regions.

ANOVAs were used to test for differences in leaf area index among the three different types of specimens (Table 1): herbarium specimens, modern specimens in sites without deer and modern specimens in sites with deer. To control for the unequal variance among the three specimen types (Bartlett test; $P < 0.0001$; Fig. 2), a variance weight was incorporated for specimen type using the *varIdent* function from the *nlme* package in R (Zuur et al. 2009; Pinheiro et al. 2013). The heterogeneity of variance was controlled by allowing the residuals to vary for each nominal level of specimen type, i.e., three variance parameters estimated by the model (Zuur et al. 2009). To further test whether this heteroscedasticity was due to any site-specific effect in herbarium and modern data, a second model that incorporated a heterogeneous variance for each site, and a third model that incorporated both a heterogeneous variance for site and specimen type were evaluated. To compare these three models, the Akaike's information criterion (AIC) was used. The AIC is a

measure of goodness-of-fit of the data to an estimated statistical model (Akaike 1974). The model with the smallest value of AIC is then the most likely for the data (Legendre and Legendre 2012).

All statistical tests were carried out in R version 3.0.2 (R Core Team, Vienna, Austria) using the *stats* package (R Core Team 2013) for the Welch's *t*-test and the one-way ANOVA, and the *nlme* package (Pinheiro et al. 2013) for ANOVA with variance weight.

3.3 Results

There was no significant difference for leaf area between herbarium specimens sampled ≥1971 and those sampled <1971 (Welch's *t*-test; $t = -1.19$, d.f. = 415.62, $P = 0.23$), suggesting no climate effect over time. No statistically significant difference was found between herbarium specimens grouped according to their bioclimatic region (one-way ANOVA; $F = 1.402$, $P = 0.247$), indicating no regional climate effect.

A significant effect of specimen type on leaf area was found (one-way ANOVA; $F = 384.86$, $P < 0.0001$). Heterogeneity of variance among sites was however detected, essentially explained by the fact one botanist sampled eight particularly small individuals at MRP on 18 May 1932. This heterogeneity was controlled using a weighted variance for this factor; the second model, weighted for site, had the lowest AIC (AIC for model 1 to 3: 36488, 36419 and 36423).

In deer sites, the *T. grandiflorum* populations were consistently represented by individuals with a leaf area index <60 cm^2, which differed significantly from the herbarium specimens and specimens collected in forests without deer ($P < 0.001$; Fig. 3). Very few large individuals, with a leaf area index >90 cm^2, persisted in deer sites. The distribution of *T. grandiflorum* individuals in deer sites was also skewed towards smaller plants, while the leaf area distribution for sites without deer and for herbarium specimens was more similar, including several very large individuals (>120 cm^2; Fig. 3). However, herbarium specimens contained a greater number of small to very small individuals, with a leaf area index 10–50 cm^2, than modern specimens in sites without deer.

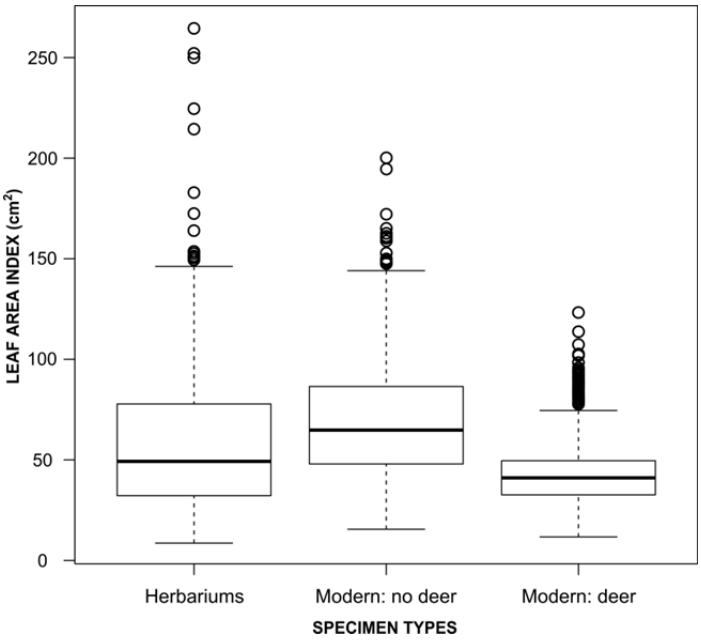

Figure 2. Distribution of leaf area index values of *T. grandiflorum* specimens from different sources (southern Québec). For each boxplot, the median (horizontal bar), 25 and 75 percentiles (box), 10 and 90 percentiles (error bars), and outlier values (circles) are indicated.

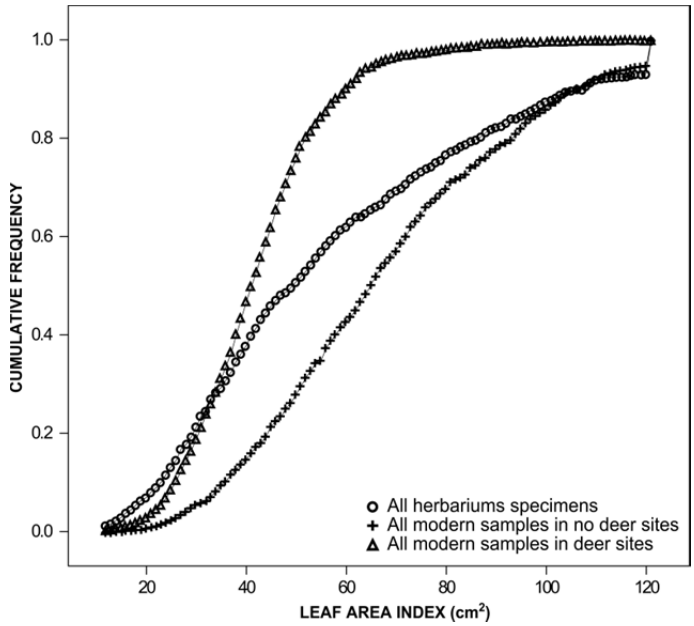

Figure 3. Cumulative frequency distributions of leaf area index values of *T. grandiflorum* specimens from different sources (southern Québec).

3.4 Discussion

No herbarium specimen of *T. grandiflorum* was specifically sampled to study the impact of deer browsing on leaf morphology. They nevertheless proved to be reliable tools for such purpose. The leaf area of modern individuals from sites with deer was clearly lower than that of modern specimens from sites without deer, which concurred with previous studies (Anderson 1994; Augustine and Frelich 1998; Knight 2003). The leaf area of modern specimens from sites with deer was also significantly lower than that of herbarium specimens. Because most herbarium specimens were sampled before 1980 (85%), i.e., before the rise of *O. virginianus* populations in southern Québec (Potvin 1994), they are thus representative of low deer density situations. Herbarium specimens can consequently be used as a reference population to reconstruct the impact of deer on plant morphology on a regional basis, in combination with modern specimens. Moreover, in southern Québec, a significant reduction of leaf area of *T. grandiflorum* is likely driven by the expansion of deer populations, since no other cause (e.g., climatic) can be involved for explaining such change.

Herbarium specimens of *T. grandiflorum* had leaf area values similar across spatial and temporal scales, which suggests that the growth of this species is not much influenced by variations of climatic and environmental conditions, at least at a regional scale. This facilitates comparisons between sites, and increases the number of specimens that can potentially be included in a reconstruction analysis, which is extremely important considering all the collection biases that can strongly influence small size samples (Lavoie 2013). Moreover, as shown in this study, gathering information on plant collectors is also important to detect (and correct) biases associated with botanists focusing on particular specimen types or sites (Lavoie et al. 2007).

Herbarium and modern specimens also indicated that *T. grandiflorum* populations in deer sites are clearly dominated by small flowering individuals, which have probably a lower reproductive success (Knight 2003). This suggests that deer is potentially jeopardizing the species persistence in high deer density forests, even in parks created to ensure the flora conservation. Particularly striking is the total absence, in forest sites with deer, of large individuals with a leaf area >120 cm^2. Although this absence is expected at high deer densities ~25–35 deer/km^2 (Augustine and Frelich 1998), our study suggests that even densities as low as 8 deer/km^2 can lead to the disappearance of a particular size class. The exact contribution of these very large individuals to the long-term persistence of white trillium populations is unknown, but their absence clearly indicates an impoverishment of natural diversity.

In conclusion, herbarium specimens represent a unique and inexpensive alternative to traditional methods used to assess the impact of large herbivores on forest flora, usually based on the establishment of exclosures (Augustine and Frelich 1998; Webster et al. 2005) or experimental clipping manipulations (Rooney and Waller 2001; Knight 2003; Knight 2007). The greatest advantage of herbarium specimen over the other methods remains the spatial coverage, potentially continental wide, an option hardly conceivable for the other types of studies. Collecting herbarium specimens throughout the entire range of a species offers a much broader perspective on the impact of herbivores on plant fitness. Unfortunately, this possibility is seriously hampered by the decline of herbarium specimen collecting throughout North America (Prather et al., 2004; Lavoie and Lachance, 2006; Lavoie et al., 2012). For example, the low number of records in Québec after 1980, when the deer populations began to rise, limits herbarium collections to a reference database (low deer density), and additional field surveys are thus necessary to evaluate the impacts of browsing. Museum collections remain highly valuable, but their potential would be much greater if recent specimens were also available for comparison.

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Chapitre 4: Conclusion générale

La création de territoires protégés vise à préserver l'intégrité écologique des écosystèmes, en garantissant la viabilité des populations d'espèces vulnérables et d'intérêt, en plus d'assurer la pérennité des fonctions écologiques des systèmes naturels concernés (Parrish et al. 2003; Timko & Innes 2009). Le premier chapitre de ce mémoire a pourtant souligné l'existence d'importantes lacunes dans la capacité des aires protégées à atteindre ces objectifs. Devant les succès de conservation mitigés documentés à travers le monde, il importe donc d'étudier l'évolution de la biodiversité au sein des aires protégées, particulièrement celles situées en périphérie des grands centres urbains. La capacité de ces aires protégées à préserver de manière pérenne la diversité locale, en dépit de la multiplicité de menaces associées à l'urbanité, est largement méconnue, bien qu'elles soient pourtant considérées comme d'importants refuges écologiques. Au Québec par exemple, les plus petites aires protégées se retrouvent dans la portion méridionale de la province, là où le morcellement du territoire par l'urbanisation, l'agriculture et le réseau routier est le plus marqué (Ministère du Développement durable, de l'Environnement et des Parcs 2009; Brassard 2011). Aucune étude n'a pourtant porté sur le potentiel de conservation de ces aires protégées à travers les décennies, bien qu'elles recèlent souvent une biodiversité digne de mention. En ce sens, notre étude au parc national du Mont-Saint-Bruno est la première à avoir véritablement mesuré le succès de conservation d'une petite aire protégée périurbaine, et ce, sur une période de 35 ans. Une telle perspective historique a d'ailleurs permis de cerner les principaux changements floristiques, et d'en identifier les facteurs présumés.

Le second chapitre de ce mémoire a permis de révéler qu'en dépit d'un nombre croissant de visiteurs, d'une importante progression d'espèces exotiques envahissantes dans la région, d'une tempête de verglas historique et de la surabondance de cerfs de Virginie, aucune espèce végétale du parc national du Mont-Saint-Bruno n'a subi de déclin significatif au cours des 35 dernières années. La diversité floristique locale a également bondi au cours de cette période, sans le concours des espèces exotiques. Ces résultats s'apparentent à ceux obtenus à la suite de reconstitutions historiques dans de petits parcs ruraux (Lavoie & Saint-Louis 2008; Bourdages & Lavoie 2011), davantage qu'à ceux enregistrés dans de petits parcs urbains (p. ex. Drayton & Primack 1996; Turner et al. 1996; DeCandido 2004). Ces reconstitutions floristiques ont en effet démontré que les parcs ruraux parviennent à préserver efficacement leur flore, mais ne sont pas complètement imperméables à l'introduction d'espèces exotiques. Bourdages et Lavoie (2011) ont émis l'hypothèse que les restrictions d'accès au parc, de même que l'encadrement serré des

visiteurs, ont eu davantage d'influence sur le maintien de l'intégrité de la flore du parc étudié (Île Bonaventure, Québec) que la taille de celui-ci. Cette hypothèse peut d'ailleurs être transposée au parc national du Mont-Saint-Bruno, puisque son statut contribue à encadrer de manière restrictive les activités dans son enceinte, en plus d'attirer des usagers probablement déjà sensibles à sa mission de conservation.

Simultanément à cet enrichissement, la diversité bêta a toutefois enregistré un déclin significatif, les assemblages floristiques tendant désormais à se ressembler indépendamment de l'habitat forestier étudié. Malgré cette homogénéisation taxonomique, la diversité fonctionnelle de la flore forestière s'est accrue, la rendant probablement plus résiliente face aux événements perturbateurs. Cette diversité fonctionnelle pourrait d'ailleurs contribuer à renforcer la résistance de la flore aux invasions botaniques, puisqu'une grande diversité de traits fonctionnels accroît la productivité, limitant ainsi les ressources disponibles pour les espèces invasives (Mason et al. 2005). Ce faisant, malgré l'accroissement du nombre de visiteurs – et conséquemment, du nombre de vecteurs potentiels de propagation –, la progression des espèces exotiques envahissantes pourrait être contenue ou ralentie. La situation de ces plantes invasives au parc national du Mont-Saint-Bruno devra néanmoins faire l'objet d'un suivi serré, puisque certaines des espèces recensées sont hautement compétitives (p.ex. *Alliaria petiolata, Rhamnus cathartica*).

Mes résultats ont également démontré une progression significative de traits fonctionnels associés à des habitats forestiers intensément broutés, suggérant une certaine influence du cerf de Virginie sur la composition de la flore forestière. Il est néanmoins encore trop tôt pour déterminer si l'influence de ce grand herbivore sur la flore du parc conduira à l'extirpation d'espèces d'intérêt (p. ex. *Trillium grandiflorum*, Chapitre 3) tel qu'observé dans certaines forêts des États-Unis (Rooney 2001; Horsley et al. 2003; Holmes & Webster 2011; Begley-Miller et al. 2014), d'autant plus que plusieurs espèces végétales étudiées sont rhizomateuses, ce qui leur confère une certaine tolérance face au broutement (Frerker et al. 2013; Bachand et al. 2014). Des mesures de répression devraient néanmoins être mises en place dès maintenant, la situation étant encore réversible. Cependant, le contrôle des cerfs de Virginie dans les milieux périurbains est complexe, les risques d'accidents liés à la chasse étant élevés. Un projet-pilote de chasse contrôlée à l'île aux Hérons, en périphérie de l'île de Montréal, s'est d'ailleurs déroulé en 2014 afin de tester l'efficacité de la chasse à l'arc et à l'arbalète dans le contrôle des cerfs de Virginie (Portail Québec 2014; Despatie 2014). Les résultats devraient permettre de mieux cibler les actions à prendre au parc national du Mont-Saint-Bruno.

D'autre part, ce mémoire a aussi permis de révéler que les effets de l'épisode de verglas de 1998 sur la flore forestière sont désormais imperceptibles, malgré l'ampleur et l'intensité historiques de cette tempête. Au cours des quinze dernières années, la canopée semble ainsi s'être refermée, atténuant les possibles impacts de cette tempête sur la voûte forestière. Le développement de la canopée inférieure (c.-à-d. gaules), probablement favorisé par un apport soudain en lumière au sol suite à la création de trouées, semble désormais être un des principaux vestiges de cette tempête. Quant à l'impact des sentiers sur la végétation de sous-bois, il semble tout aussi imperceptible. À ce sujet, il importe de mentionner que les sentiers pédestres du parc national du Mont-Saint-Bruno, bien qu'aménagés (p. ex. recouverts de gravier), sont étroits, recouverts par une canopée dense. Ce facteur semble d'ailleurs être déterminant dans la préservation de l'intégrité de la flore locale, l'ouverture de la canopée par de larges sentiers prédisposant les forêts à l'introduction d'espèces exotiques et à une modification des conditions édaphiques (Lajeunesse et al. 1997; Baret & Strasberg 2005). En ce sens, nos recommandations générales sont ii) d'encourager, en tout temps, la création de sentiers étroits, limitant l'ouverture de la canopée et ii) de prévoir des secteurs sans aménagements, afin de limiter les corridors potentiels de dispersion des espèces exotiques.

Enfin, l'étude présentée dans le troisième chapitre a, quant à elle, permis de confirmer l'intérêt des herbiers botaniques dans l'étude de l'impact du cerf de Virginie sur la morphologie de plantes broutées. Cette méthode alternative est simple, rapide et peu coûteuse, comparativement à la construction d'exclos, au broutement artificiel («clipping») ou à la saisie de données sur plusieurs années. En ce sens, il s'agit d'une méthode toute désignée pour la recherche scientifique au sein d'aires protégées, étant nettement moins invasive que les méthodes traditionnelles. Les herbiers botaniques fournissent ainsi une population de référence constituée de spécimens en provenance de territoires variés (conditions environnementales multiples), accessibles gratuitement et couvrant une longue période de récolte, permettant ainsi de documenter l'évolution morphologique d'espèces en condition d'herbivorie.

Malgré un succès de conservation certain, la flore au parc national du Mont-Saint-Bruno devra néanmoins faire face à de multiples défis au cours des prochaines années, voire décennies. Outre la surabondance de cerfs et les plantes exotiques envahissantes qui maintiendront la pression, la flore forestière devra composer avec l'évolution bien incertaine du climat, l'arrivée d'insectes exotiques (p. ex. agrile du frêne) ou même, la modification profonde de la dynamique forestière naturelle. En effet, le hêtre à grandes feuilles pourrait bien s'imposer davantage sur la

colline, favorisé par sa grande tolérance à l'ombre et sa capacité de se reproduire végétativement (Beaudet et al. 1999), au détriment de l'érable à sucre. La progression du hêtre à grandes feuilles au cours des 35 dernières années dans les trois strates forestières (c.-à-d. semis, gaules, arbres) et la difficile régénération de l'érable à sucre renforcent d'ailleurs cette idée. L'étude du Boisé-des-Muir (Brisson et al. 1992), forêt précoloniale préservée dans le Haut-Saint-Laurent, a justement remis en doute l'idée de l'érablière à caryer cordiforme comme communauté climacique de cette région (selon Grandtner 1966), soulevant plutôt l'importance du hêtre à grandes feuilles dans la composition des forêts anciennes du sud du Québec. En effet, au Boisé-des-Muir, cette espèce serait en voie de dominer l'érable à sucre, donnant l'impression d'une forêt transitoire et immature (Brisson et al. 1992). L'étude des archives de vente de bois par Bouchard et al. (1989) a également révélé que le hêtre à grandes feuilles était plus abondant avant la colonisation du Haut-Saint-Laurent. Ce faisant, la forêt précoloniale du sud du Québec était probablement une érablière sucrière à hêtre à grandes feuilles, plutôt qu'une érablière à caryer, cette dernière résultant plutôt de perturbations humaines (climax anthropique) (Brisson et al. 1994). La forêt du mont Saint-Bruno pourrait ainsi évoluer vers une érablière sucrière à hêtre à grandes feuilles (hypothèse partagée par Donald Rodrigue, biologiste garde-parc au parc national du Mont-Saint-Bruno), où la luminosité est faible et où la litière au sol est plus acide, limitant la richesse du cortège floristique (Brisson et al. 1992). Quoiqu'il en soit, pour l'heure, le parc national du Mont-Saint-Bruno a démontré son efficacité à protéger efficacement sa flore forestière; l'avenir nous dira si cette dernière saura résister aux futures fluctuations de son environnement.

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Appendix A

Hypothesized drivers of plant community change and expected shifts in plant functional traits for understorey plant species found at Mont-Saint-Bruno National Park [References are in brackets].

	Drivers of change			
Functional response traits	**Edge effect**	**Deer grazing**	**Succession**	**Ice storm**
Status	Exotic ↑			
Tolerance to disturbance	High tolerance ↑	High tolerance ↑	Low tolerance ↑	
Life form		Fern, grass, sedge↑ [13, 14, 15, 16, 17]		
Life cycle	Perrenial ↑ [1, 2]		Perennial ↑	
Rhizome		↑ [18, 19]		
Storage organ		↑ [18, 20, 21]		
Vegetative propagation	↑ [1, 2, 3]	↑ [18, 19, 3]		↑ [30, 3]
Seed dispersal vector	Biotic ↑ [4, 5, 6]	Abiotic ↑ [18]		
Light requirement	Shade intolerant ↑ [7, 8]		Shade tolerant ↑ [29]	Shade intolerant ↑ [30, 31, 32]
Maximum height	Tall species ↑ [9, 10, 11]	Small species ↑ [22, 23, 24]		
Palatability		Avoided or rarely browsed species ↑ [25, 26, 27, 28]		
Dispersal strategy	> one strategy ↑ [12]			> one strategy ↑ [12]

Appendix A. Continued

Explanation	Reference
1. Short-lived species (high turnover rates) are more vulnerable to habitat fragmentation than clonal long-lived species (p. 561).	Lindborg, R. 2007. Evaluating the distribution of plant life-history traits in relation to current and historical landscape configurations. Journal of Ecology 95: 555-564.
2. A lot of forest plant species are long-lived perennials that can form remnant populations by clonal growth, then exhibiting a lower susceptibility to habitat fragmentation (p.730).	Honnay, O., Jacquemyn, H., Bossuyt, B. & Hermy, M. 2004. Forest fragmentation effects on patch occupancy and population viability of herbaceous plant species. New Phytologist 166: 723-736.
3. Vegetative reproduction is an important mechanism of persistence despite natural/anthropogenic disturbances.	Bond, W.J. & Midgley, J.J. 2001. Ecology of sprouting in woody plants: the persistence niche. Trends in Ecology and Evolution 16: 45-51.
4. Metzger found a positive relation between zoochorous species richness and boundary complexity indices in its study, indicating that boundaries may favor the dispersion of zoochorous species (p. 1157).	Metzger, J.-P. 2000. Tree functional group richness and landscape structure in a brazilian tropical fragmented landscape. Ecological Applications 10: 1147-1161.
5. LDD (long distance dispersal) mechanisms (wind, birds) can greatly increase the ability of species to migrate through fragmented landscapes (p. 397).	Pearson, R.G. & Dawson, T.P. 2005. Long-distance plant dispersal and habitat fragmentation: identifying conservation targets for spatial landscape planning under climate change. Biological Conservation 123: 389-401.
6. Animal-dispersed species are generally less vulnerable to decreased forest cover than wind-dispersed species (p. 1503).	Montoya, D., Zavala, M.A., Rodriguez, M.A. & Purves, D.W. 2008. Animal versus wind dispersal and the robustness of tree species to deforestation. Science 320: 1502-1504.
7. Forest edge can lead to more high light, favoring shade intolerant species (p. 1115).	Metzger, J.P. 2000. Tree functional group richness and landscape structure in a Brazilian tropical fragmented landscape. Ecological Applications 10: 1147-1161.
8. The microclimate at the forest edge is characterized by increased light penetration, increased air and soil temperature (…), which directly affects population dynamics of the occurring plant species (p. 729).	Honnay, O., Jacquemyn, H., Bossuyt, B. & Hermy, M. 2004. Forest fragmentation effects on patch occupancy and population viability of herbaceous plant species. New Phytologist 166: 723-736.
9. Small species tend to be more negatively affected by fragmentation than tall species, as they have lower competitive ability for light (p. 905).	Marini, L., Bruun, H.H., Heikkinen, R.K., Helm, A., Honnay, O., Krauss, J., Kühn, I., Lindborg, R., Pärtel, M. & Bommarco, R. 2012. Traits related to species persistence and dispersal explain changes in plant communities subjected to habitat loss. Diversity and Distributions 18: 898-908.

Appendix A. Continued

Explanation	Reference
10. Kolb and Diekmann found that overall, small species tended to be more negatively affected by decreased patch size (p. 936-937).	Kolb, A. & Diekmann, M. 2005. Effects of life-history traits on responses of plant species to forest fragmentation. Conservation Biology 19: 929-938.
11. At high density, the development of size hierarchies can be caused by unequal light interception by large versus small individuals. Overtopping allows competing for light (p. 453).	Schwinning, S. & Weiner. J. 1998. Mechanisms determining the degree of size asymmetry in competition among plants. Oecologia 113: 447-455.
12. Larger number of potential dispersal vectors indicates that species have more opportunities for long-distance dispersal, and are thus less vulnerable to the availability of single dispersal vectors. (p. 774).	Ozinga, W.A., Bekker, R.M., Schaminée, J.H.P. & Groenendael, J.M.V. 2004. Dispersal potential in plant communities depends on environmental conditions. Journal of Ecology 92: 767-777.
13. As local deer browsing increases, understory herb community diversity declines, while ferns, grasses, sedges, and rushes become dominant (p. 169).	Rooney, T.P. & Waller, D.M. 2003. Direct and indirect effects of white-tailed deer in forest ecosystems. Forest Ecology and Management 181: 165-176.
14. Many ferns are avoided by deer (not all), possibly because of leaf tissue chemistry.	Rooney, T. & Dress, W. 1997. Species loss over sixty-six years in the ground layer vegetation of heart's content, an old-growth forest in Pennsylvania, USA. Natural Areas Journal 17: 297-305.
15. Excessive deer browsing can create fern parks, i.e., forests dominated by ferns in the understorey and no shrub or sapling layer (p. 205).	Rooney, T.P. 2001. Deer impacts on forest ecosystems: a North American perspective. Forestry 74: 201-208.
16. Most graminoids have basal meristems and silica in their tissues, making them relatively tolerant of herbivory (p. 854).	Coughenour, M.B. 1985. Graminoid responses to grazing by large herbivores: adaptations, exaptations, and interacting processes. Annals of the Missouri Botanical Garden 72: 852-863.
17. Rooney found that, with deer present, grasses and sedges can account for more than 50% of plants on ground cover (p. 108).	Rooney, T.P. 2009. High white-tailed deer densities benefit graminoids and contribute to biotic homogenization of forest ground-layer vegetation. Plant Ecology 202: 103-111.
18. In high deer density sites, Bachand et al. found that plant species that reproduce mainly vegetatively, or that have rhizomes or storage organs, are more abundant. Exotic species were also associated to those sites.	Bachand, M., Pellerin, S., Moretti, M., Aubin, I., Tremblay, J.-P., Côté, S.D. & Poulin, M. 2014. Functional Responses and Resilience of Boreal Forest Ecosystem after Reduction of Deer Density. PLoS ONE 9: e90437.

Appendix A. Continued

Explanation	Reference
19. Wild sarsaparilla (*Aralia nudicaulis*) has increased in abundance with browsing at Isle Royale National Park, probably because this species can reproduce by rhizomes and has the ability to produce clonal clusters (p. 61).	Frerker, K., Sonnier, G. & Waller, D.M. 2013. Browsing rates and ratios provide reliable indices of ungulate impacts on forest plant communities. Forest Ecology and Management 291: 55-64.
20. Deer consume preferably the larger *Trillium grandiflorum* plants, but this foraging usually does not kill plants probably because they have large, below-ground storage organs (p. 107).	Anderson, R.C. 1994. Height of white-flowered trillium (*Trillium grandiflorum*) as an index of deer browsing intensity. Ecological Applications 4: 104-109.
21. Some traits can benefit to grazed plants: basal meristems, small stature, deciduous shoots, belowground nutrient reserves, and rapid transpiration and growth. Reserves allow the regrowth after defoliation (p. 854).	Coughenour, M.B. 1985. Graminoid responses to grazing by large herbivores: adaptations, exaptations, and interacting processes. Annals of the Missouri Botanical Garden 72: 852-863.
22. Browsing pressure can reduce forb stature and releases them from competition (p. 62).	Frerker, K., Sonnier, G. & Waller, D.M. 2013. Browsing rates and ratios provide reliable indices of ungulate impacts on forest plant communities. Forest Ecology and Management 291: 55-64.
23. A shorter plant is less likely to have a large proportion of its leaves browsed by large herbivores (p. 854).	Coughenour, M.B. 1985. Graminoid responses to grazing by large herbivores: adaptations, exaptations, and interacting processes. Annals of the Missouri Botanical Garden 72: 852-863.
24. Dobson and Blossey attribute the lack of consumption on tree seedlings to their small stature. They expect consumptive deer effects to become increasingly important as slow-growing perennials and seedlings reach the browsable 'molar zone' (> 10 cm) (p. 161).	Dobson, A. & Blossey, B. 2015. Earthworm invasion, white-tailed deer and seedling establishment in deciduous forests of north-eastern North America. Journal of Ecology 103: 153-164.
25. White-tailed deer act as a biotic filter, causing the disappearance of preferred species and the dominance of avoided or browsed-resilient ones.	Begley-Miller, D.R., Hipp, A.L., Brown, B.H., Hahn, M. & Rooney, T.P. 2014. White-tailed deer are a biotic filter during community assembly, reducing species and phylogenetic diversity. AoB PLANTS 6: plu030.
26. Deer browsing can affect vegetation by facilitating the dominance of unpreferred and browse-resilient species (p. 114).	Horsley, S.B., Stout, S.L. & DeCalesta, D.S. 2003. White-tailed deer impact on the vegetation dynamics of a northern hardwood forest. Ecological Applications 13: 98-118.
27. White-tailed deer can drive biotic homogenization in forest understory communities by promoting sedges and grasses (generalist species).	Rooney, T.P. 2009. High white-tailed deer densities benefit graminoids and contribute to biotic homogenization of forest ground-layer vegetation. Plant Ecology 202: 103-111.

Appendix A. Concluded

Explanation	Reference
28. In the understorey, high deer densities caused increased fern domination, decreased seedlings and forb cover and diminished angiosperm richness (p. 5).	Nuttle, T., Royo, A.A., Adams, M.B. & Carson, W.P. 2013. Historic disturbance regimes promote tree diversity only under low browsing regimes in eastern deciduous forest. Ecological Monographs 83: 3-17.
29. Maturation of forests can reduce light levels in the understorey, favoring shade tolerant species.	Weaver, M. & M. Kellman. 1981. The effects of forest fragmentation on woodlot tree biotas in southern Ontario. Journal of Biogeography 8: 199-210.
30. Canopy gaps could be created after an ice storm, favoring shade-intolerant shrubs and herbs in taller gaps. Vegetative reproduction is also again likely to predominate, with minor contributions from seeds (p. 1279).	Roberts, M.R. 2004. Response of the herbaceous layer to natural disturbance in North American forests. Canadian Journal of Botany 82: 1273-1283.
31. In a mature woodland at the Queen's University Biological Station (in Eastern Ontario), due to the 1998 ice storm, crown damages to upper canopy trees increased canopy openness from 10% to 41% (p. 204).	Aarssen, L.W. & Francq, A.E. 2004. Effects of ice storm canopy gaps on shoot architecture in young sugar maple (*Acer saccharum*). Écoscience 11: 201-208.
32. When ice storms are severe, they can delay forest succession by creating canopy openings and favoring less shade-tolerant species (p. 207).	DeSteven, D., Kline, J. & Matthiae, P.E. 1991. Long-term changes in a Wisconsin *Acer–Fagus* forest in relation to glaze disturbance. Journal of Vegetation Science 2: 201-208.

Appendix B

Trait values for the understorey plant species found in the forest of the Mont-Saint-Bruno National Park in 1977 and 2013. See Table 1 for abbreviations of traits.

	MH	RH	ST	LC	GS	FE	FO	VI	SH	VP	AD	BD	DS	LR	SS	TD	PA
Acer spicatum	4	0	0	3	0	0	0	0	1	0	1	0	1	2	1	1	3
Actaea pachypoda	2	1	0	3	0	0	1	0	0	0	0	1	2	3	1	3	1
Actaea rubra	2	1	0	3	0	0	1	0	0	0	0	1	2	3	1	3	1
Adiantum pedatum	2	1	0	3	0	1	0	0	0	0	1	0	1	3	1	2	1
Ageratina altissima	3	1	0	3	0	0	1	0	0	0	1	0	1	2	1	2	1
Agrimonia gryposepala	3	0	0	3	0	0	1	0	0	0	0	1	1	2	1	1	1
Alliaria petiolata	3	0	0	2	0	0	1	0	0	0	1	1	3	2	2	1	1
Alnus rugosa	5	1	0	3	0	0	0	0	1	1	1	0	2	1	1	2	1
Amelanchier sp.	5	0	0	3	0	0	0	0	1	1	0	1	2	3	1	2	2
Amphicarpaea bracteata	3	0	0	1	0	0	0	1	0	0	1	1	4	2	1	2	3
Anaphalis margaritacea	2	1	0	3	0	0	1	0	0	0	1	0	1	1	1	1	1
Anemone americana	1	1	0	3	0	0	1	0	0	1	0	1	2	3	1	2	1
Apios americana	4	0	1	3	0	0	0	1	0	1	1	0	1	3	1	1	2
Apocynum androsaemifolium	3	1	0	3	0	0	1	0	0	1	1	0	1	1	1	1	1
Aquilegia canadensis	2	0	0	3	0	0	1	0	0	0	1	0	1	1	1	2	1
Aralia nudicaulis	1	1	0	3	0	0	1	0	0	1	0	1	2	3	1	2	3
Aralia racemosa	3	1	0	3	0	0	1	0	0	1	0	1	2	3	1	3	3
Arctium minus	3	0	0	2	0	0	1	0	0	0	0	1	1	1	2	1	2
Ariseama triphyllum	2	0	1	3	0	0	1	0	0	1	0	1	1	3	1	2	1
Asarum canadense	1	1	0	3	0	0	1	0	0	1	0	1	1	3	1	2	1
Athyrium filix-femina	2	1	0	3	0	1	0	0	0	1	1	0	2	3	1	2	1
Berberis thunbergii	3	0	1	3	0	0	0	0	1	0	0	1	2	1	2	1	1
Bidens frondosa	2	0	0	1	0	0	1	0	0	0	1	1	2	1	1	1	1
Botrypus virginianus	2	1	0	3	0	1	0	0	0	0	1	0	1	3	1	2	2

Appendix B. Continued

	MH	RH	ST	LC	GS	FE	FO	VI	SH	VP	AD	BD	DS	LR	SS	TD	PA
Calla palustris	1	1	0	3	0	0	1	0	0	0	1	0	2	3	1	3	1
Carex spp.	2	1	0	3	1	0	0	0	0	1	0	1	1	3	1	2	1
Caulophyllum thalictroides	2	1	0	3	0	0	1	0	0	1	0	1	1	3	1	2	1
Chelone glabra	2	1	0	3	0	0	1	0	0	0	1	0	2	1	1	3	1
Circaea canadensis	2	1	0	3	0	0	1	0	0	1	0	1	1	2	1	1	3
Claytonia caroliniana	1	1	0	3	0	0	1	0	0	1	0	1	1	3	1	2	2
Coleus sp.	2	1	0	3	0	0	1	0	0	1	1	0	1	2	2	1	1
Conopholis americana	1	0	1	3	0	0	1	0	0	0	0	1	1	3	1	3	3
Convallaria majalis	1	1	0	3	0	0	1	0	0	1	0	1	1	3	2	1	1
Coptis trifolia	1	1	0	3	0	0	1	0	0	1	0	1	1	3	1	2	1
Corallorhiza maculata	2	1	0	3	0	0	1	0	0	1	1	0	1	3	1	2	3
Cornus alternifolia	5	0	0	3	0	0	0	0	1	1	1	1	3	2	1	1	2
Cryptotaenia canadensis	2	0	0	3	0	0	1	0	0	0	0	1	1	3	1	1	2
Cystopteris fragilis	2	1	0	3	0	1	0	0	0	0	1	0	1	2	1	1	2
Deparia acrostichoides	2	1	0	3	0	1	0	0	0	1	1	0	1	2	1	2	1
Desmodium canadense	3	0	0	3	0	0	1	0	0	0	0	1	1	2	1	1	2
Dicentra canadensis	1	1	1	3	0	0	1	0	0	0	0	1	1	3	1	3	1
Dicentra cucullaria	1	1	1	3	0	0	1	0	0	0	0	1	1	3	1	3	1
Diervilla lonicera	3	1	0	3	0	0	0	0	1	1	0	1	1	2	1	2	3
Dirca palustris	3	1	0	3	0	0	0	0	1	0	0	1	1	3	1	3	1
Dryopteris carthusiana	2	1	0	3	0	1	0	0	0	1	1	0	1	3	1	2	1
Dryopteris marginalis	2	1	0	3	0	1	0	0	0	1	1	0	2	3	1	2	1
Epifagus virginiana	2	0	0	1	0	0	1	0	0	0	1	0	1	3	1	3	1
Epipactis helleborine	2	1	0	3	0	0	1	0	0	1	1	0	1	3	2	1	2
Equisetum fluviatile	3	1	0	3	0	1	0	0	0	1	1	0	1	3	1	3	1
Equisetum pratense	2	1	0	3	0	1	0	0	0	1	1	0	1	2	1	3	1
Equisetum sylvaticum	2	1	0	3	0	1	0	0	0	1	1	0	1	2	1	2	1

Appendix B. Continued

	MH	RH	ST	LC	GS	FE	FO	VI	SH	VP	AD	BD	DS	LR	SS	TD	PA
Erythronium americanum	1	1	1	3	0	0	1	0	0	1	0	1	1	3	1	2	3
Euonymus alatus	4	0	0	3	0	0	0	0	1	0	1	1	2	3	2	1	1
Eurybia macrophylla	2	1	0	3	0	0	1	0	0	1	1	1	2	3	1	2	3
Eutrichium maculatum	3	1	0	3	0	0	1	0	0	0	1	0	1	1	1	2	2
Fragaria virginiana	1	1	0	3	0	0	1	0	0	1	0	1	2	1	1	1	3
Frangula alnus	4	0	1	3	0	0	0	0	1	0	1	1	4	2	2	1	1
Galeopsis tetrahit	2	0	0	1	0	0	1	0	0	0	1	1	4	1	2	1	1
Galium lanceolatum	2	1	0	3	0	0	1	0	0	0	0	1	1	3	1	2	2
Galium palustre	2	1	0	3	0	0	1	0	0	1	1	1	2	2	1	1	1
Galium trifidum	2	1	0	3	0	0	1	0	0	1	0	1	2	2	1	2	2
Hieracium paniculatum	2	0	0	3	0	0	1	0	0	0	1	0	1	3	1	3	2
Hieracium umbellatum	3	0	0	3	0	0	1	0	0	0	1	0	1	3	1	2	3
Huperzia lucidula	1	0	1	3	0	1	0	0	0	1	1	0	1	3	1	2	1
Hylodesmum glutinosum	3	0	0	3	0	0	1	0	0	0	0	1	2	2	1	2	3
Hylodesmum nudiflorum	2	0	0	3	0	0	1	0	0	0	1	1	2	2	1	3	3
Hylotelephium telephium	2	1	0	3	0	0	1	0	0	1	1	0	1	2	2	1	1
Ilex mucronata	4	0	0	3	0	0	0	0	1	0	0	1	1	2	1	3	3
Impatiens capensis	2	0	0	1	0	0	1	0	0	0	1	0	1	2	1	1	3
Iris versicolor	2	1	0	3	0	0	1	0	0	0	1	0	1	1	1	2	1
Lonicera canadensis	3	0	0	3	0	0	0	0	1	0	0	1	1	3	1	2	3
Lonicera tatarica	3	0	0	3	0	0	0	0	1	0	0	1	2	2	2	1	2
Lycopodium obscurum	1	1	0	3	0	0	1	0	0	0	1	0	1	3	1	1	1
Lycopus americanus	2	1	1	3	0	1	0	0	0	0	1	1	2	2	1	2	1
Lycopus uniflorus	2	1	1	3	0	0	1	0	0	0	1	0	1	2	1	1	1
Lysimachia borealis	1	1	0	3	0	0	1	0	0	0	1	1	2	3	1	2	2
Lysimachia thyrsiflora	2	1	0	3	0	0	1	0	0	0	1	0	2	1	1	2	1

Appendix B. Continued

	MH	RH	ST	LC	GS	FE	FO	VI	SH	VP	AD	BD	DS	LR	SS	TD	PA
Maianthemum canadense	1	1	0	3	0	0	1	0	0	1	0	1	2	3	1	2	3
Maianthemum racemosum	2	1	0	3	0	0	1	0	0	1	0	1	2	3	1	2	3
Matteuccia struthiopteris	3	1	0	3	0	1	0	0	0	0	1	0	2	3	1	1	1
Medeola virginiana	2	1	0	3	0	0	1	0	0	1	0	1	1	3	1	3	3
Mitchella repens	1	1	0	3	0	0	1	0	0	1	0	1	2	3	1	2	2
Mitella diphylla	2	1	0	3	0	0	1	0	0	0	1	0	1	3	1	3	2
Monotropa uniflora	1	0	0	3	0	0	1	0	0	0	1	0	2	3	1	2	1
Nabalus altissima	3	0	1	3	0	0	1	0	0	0	1	0	1	3	1	2	2
Oclemena acuminata	2	1	0	3	0	0	1	0	0	0	1	0	1	3	1	2	3
Onoclea sensibilis	3	1	0	3	0	1	0	0	0	0	1	0	2	2	1	1	1
Osmorhiza claytonii	2	1	0	3	0	0	1	0	0	0	1	1	3	3	1	2	1
Osmunda claytoniana	3	1	0	3	0	1	0	0	0	0	1	0	2	3	1	2	1
Osmunda regalis	3	1	0	3	0	1	0	0	0	0	1	0	2	2	1	2	1
Osmundastrum cinnamomeum	3	1	0	3	0	1	0	0	0	0	1	0	2	3	1	2	1
Oxalis stricta	1	1	0	3	0	0	1	0	0	1	1	0	2	1	2	1	2
Panax quinquefolius	2	1	0	3	0	0	1	0	0	0	1	1	3	3	1	3	3
Parthenocissus quinquefolia	3	1	0	3	0	0	0	1	0	1	0	1	1	2	1	2	1
Phegopteris connectilis	2	1	0	3	0	1	0	0	0	1	1	0	2	3	1	2	1
Pilea pumila	2	0	0	1	0	0	1	0	0	0	1	0	1	3	1	2	3
Pilosella officinarum	2	1	0	3	0	0	1	0	0	1	1	0	1	1	2	1	2
Poaceae spp.	3	0	0	3	1	0	0	0	0	0	1	0	1	3	1	3	3
Polygonatum pubescens	2	1	0	3	0	0	1	0	0	0	0	1	1	3	1	2	3
Polypodium virginianum	2	1	0	3	0	1	0	0	0	1	1	0	2	3	1	3	1
Polystichum acrostichoides	2	1	0	3	0	1	0	0	0	1	1	0	2	3	1	2	2
Potentilla simplex	2	1	1	3	0	0	1	0	0	0	1	0	1	1	1	1	1
Prunus virginiana	5	1	0	3	0	0	0	0	1	1	0	1	1	2	1	1	3
Pteridium aquilinum	2	1	0	3	0	1	0	0	0	1	1	0	2	1	1	1	2
Pyrola chlorantha	1	1	0	3	0	0	1	0	0	1	1	0	1	3	1	3	1

Appendix B. Continued

	MH	RH	ST	LC	GS	FE	FO	VI	SH	VP	AD	BD	DS	LR	SS	TD	PA
Pyrola elliptica	1	1	0	3	0	0	1	0	0	1	1	0	1	3	1	2	1
Ranunculus abortivus	2	0	0	3	0	0	1	0	0	0	1	0	1	1	1	1	1
Rhamnus cathartica	5	0	0	3	0	0	0	0	1	0	1	1	4	2	2	1	1
Rhus typhina	5	1	0	3	0	0	0	0	1	1	0	1	1	1	1	1	3
Ribes cynosbati	3	0	0	3	0	0	0	0	1	0	0	1	2	3	1	2	2
Ribes lacustre	3	1	0	3	0	0	0	0	1	0	0	1	2	3	1	2	2
Rubus allegheniensis	3	1	0	3	0	0	0	0	1	1	0	1	2	1	1	1	3
Rubus idaeus	3	1	0	3	0	0	0	0	1	1	0	1	2	1	1	1	3
Rubus pubescens	2	1	0	3	0	0	0	0	1	1	0	1	2	3	1	2	2
Sambucus racemosa	1	1	0	3	0	0	0	0	1	0	0	1	2	2	1	1	2
Sanguinaria canadensis	1	1	0	3	0	0	1	0	0	1	0	1	1	3	1	2	1
Sanicula marilandica	3	0	0	3	0	0	1	0	0	0	0	1	1	2	1	2	2
Scutellaria galericulata	2	1	0	3	0	0	1	0	0	0	1	1	2	2	1	2	1
Scutellaria lateriflora	2	1	0	3	0	0	1	0	0	0	0	1	2	3	1	2	1
Solanum nigrum	2	0	0	3	0	0	1	0	0	0	0	1	1	1	2	1	1
Solidago caesia	2	1	0	3	0	0	1	0	0	1	1	0	1	3	1	2	3
Solidago canadensis	3	1	0	3	0	0	1	0	0	1	1	0	1	1	1	1	3
Solidago flexicaulis	2	1	0	3	0	0	1	0	0	1	1	0	1	3	1	2	3
Streptopus lanceolatus	2	1	0	3	0	0	1	0	0	1	0	1	1	3	1	2	3
Symphyotrichum cordifolium	2	1	0	3	0	0	1	0	0	0	1	0	1	3	1	2	2
Symphyotrichum puniceum	3	1	0	3	0	0	1	0	0	0	1	0	1	1	1	2	3
Symphyotrichum simplex	3	1	0	3	0	0	1	0	0	0	1	0	1	1	1	2	3
Taraxacum officinale	2	0	0	3	0	0	1	0	0	0	1	0	1	1	2	1	3
Thalictrum dioicum	2	1	0	3	0	0	1	0	0	1	1	1	2	3	1	2	1
Thelypteris noveboracensis	2	1	0	3	0	1	0	0	0	1	1	0	2	3	1	2	1
Thelypteris palustris	2	1	0	3	0	1	0	0	0	0	1	0	1	1	1	2	1

Appendix B. Concluded

	MH	RH	ST	LC	GS	FE	FO	VI	SH	VP	AD	BD	DS	LR	SS	TD	PA
Tiarella cordifolia	1	0	0	3	0	0	1	0	0	0	1	0	1	3	1	3	1
Toxicodendron radicans	2	1	0	3	0	0	0	1	0	1	0	1	1	3	1	1	2
Trillium erectum	2	1	0	3	0	0	1	0	0	0	0	1	1	3	1	2	3
Trillium grandiflorum	2	1	0	3	0	0	1	0	0	0	0	1	1	3	1	2	3
Tussilago farfara	1	1	0	3	0	0	1	0	0	1	1	0	1	1	2	1	1
Urtica dioica	3	1	0	3	0	0	1	0	0	1	0	1	1	1	1	1	1
Uvularia grandiflora	2	1	0	3	0	0	1	0	0	1	0	1	1	3	1	2	3
Uvularia sessilifolia	1	1	0	3	0	0	1	0	0	1	0	1	1	3	1	2	3
Valeriana officinalis	3	1	0	3	0	0	1	0	0	0	1	0	1	1	2	1	1
Viburnum lantanoides	3	0	0	3	0	0	0	0	1	0	0	1	2	3	2	1	3
Vinca minor	1	0	0	3	0	0	0	0	1	1	1	0	1	3	2	1	1
Viola canadensis	1	1	0	3	0	0	1	0	0	1	0	1	1	3	1	2	2
Viola cucullata	1	1	0	3	0	0	1	0	0	0	0	1	2	3	1	2	2
Viola pubescens	1	1	0	3	0	0	1	0	0	1	1	1	2	3	1	2	1
Vitis riparia	3	0	0	3	0	0	0	1	0	0	0	1	1	1	1	2	2

Appendix C

Understorey plant species found in the forest of the Mont-Saint-Bruno National Park identified as 'winners' and 'no change' (2013 vs. 1977 plant surveys) according to an indicator trait analysis ($P \leq 0.05$), and their respective functional response traits. 'Winners' are classified from greatest to lowest gain in plots over time and their frequency in 2013 is also indicated. See Table 1 for abbreviations of traits.

	Plot gain	Freq. 2013	MH	RH	ST	LC	GS	FE	FO	VI	SH	VP	AD	BD	DS	LR	SS	TD	PA
Winners																			
Carex spp.	+87	100	2	1	0	3	1	0	0	0	0	1	0	1	1	3	1	2	1
Epipactis helleborine	+71	80	2	1	0	3	0	0	1	0	0	1	1	0	1	3	2	1	2
Poaceae spp.	+71	95	3	0	0	3	1	0	0	0	0	0	1	0	1	3	1	3	3
Maianthemum canadense	+66	96	1	1	0	3	0	0	1	0	0	1	0	1	2	3	1	2	3
Polygonatum pubescens	+66	111	2	1	0	3	0	0	1	0	0	0	0	1	1	3	1	2	3
Aralia nudicaulis	+65	98	1	1	0	3	0	0	1	0	0	1	0	1	2	3	1	2	3
Solidago caesia	+64	113	2	1	0	3	0	0	1	0	0	1	1	0	1	3	1	2	3
Trillium grandiflorum	+63	91	2	1	0	3	0	0	1	0	0	0	0	1	1	3	1	2	3
Ariseama triphyllum	+59	61	2	0	1	3	0	0	1	0	0	1	0	1	1	3	1	2	1
Nabalus altissima	+59	71	3	0	1	3	0	0	1	0	0	0	1	0	1	3	1	2	2
Actaea rubra	+51	59	2	1	0	3	0	0	1	0	0	0	0	1	2	3	1	3	1
Thalictrum dioicum	+44	86	2	1	0	3	0	0	1	0	0	1	1	1	2	3	1	2	1
Uvularia sessilifolia	+41	77	1	1	0	3	0	0	1	0	0	1	0	1	1	3	1	2	3
Dryopteris carthusiana	+39	45	2	1	0	3	0	1	0	0	0	1	1	0	1	3	1	2	1
Maianthemum racemosum	+35	64	2	1	0	3	0	0	1	0	0	1	0	1	2	3	1	2	3
Amphicarpaea bracteata	+33	41	3	0	0	1	0	0	0	1	0	0	1	1	4	2	1	2	3
Dryopteris marginalis	+31	37	2	1	0	3	0	1	0	0	0	1	1	0	2	3	1	2	1
Anemone americana	+23	31	1	1	0	3	0	0	1	0	0	1	0	1	2	3	1	2	1
Hylodesmum glutinosum	+21	22	3	0	0	3	0	0	1	0	0	0	0	1	2	2	1	2	3
Osmorhiza claytonii	+21	29	2	1	0	3	0	0	1	0	0	0	1	1	3	3	1	2	1
Alliaria petiolata	+19	19	3	0	0	2	0	0	1	0	0	0	1	1	3	2	2	1	1

Appendix C. Continued

	Plot gain	Freq. 2013	MH	RH	ST	LC	GS	FE	FO	VI	SH	VP	AD	BD	DS	LR	SS	TD	PA
Winners																			
Asarum canadense	+19	23	1	1	0	3	0	0	1	0	0	1	0	1	1	3	1	2	1
Monotropa uniflora	+19	19	1	0	0	3	0	0	1	0	0	0	1	0	2	3	1	2	1
Symphyotrichum cordifolium	+19	20	2	1	0	3	0	0	1	0	0	0	1	0	1	3	1	2	2
Apocynum androsaemifolium	+17	18	3	1	0	3	0	0	1	0	0	1	1	0	1	1	1	1	1
Circaea canadensis	+17	20	2	1	0	3	0	0	1	0	0	1	0	1	1	2	1	1	3
Solidago flexicaulis	+17	25	2	1	0	3	0	0	1	0	0	1	1	0	1	3	1	2	3
Sanguinaria canadensis	+16	18	1	1	0	3	0	0	1	0	0	1	0	1	1	3	1	2	1
Galium trifidum	+13	13	2	1	0	3	0	0	1	0	0	1	0	1	2	2	1	2	2
Hieracium paniculatum	+13	14	2	0	0	3	0	0	1	0	0	0	1	0	1	3	1	3	2
Hylodesmum nudiflorum	+13	15	2	0	0	3	0	0	1	0	0	0	1	1	2	2	1	3	3
Panax quinquefolius	+10	10	2	1	0	3	0	0	1	0	0	0	1	1	3	3	1	3	3
No change																			
Acer spicatum	-	-	4	0	0	3	0	0	0	0	1	0	1	0	1	2	1	1	3
Adiantum pedatum	-	-	2	1	0	3	0	1	0	0	0	0	1	0	1	3	1	2	1
Ageratina altissima	-	-	3	1	0	3	0	0	1	0	0	0	1	0	1	2	1	2	1
Amelanchier sp.	-	-	5	0	0	3	0	0	0	0	1	1	0	1	2	3	1	2	2
Athyrium filix-femina	-	-	2	1	0	3	0	1	0	0	0	1	1	0	2	3	1	2	1
Corallorhiza maculata	-	-	2	1	0	3	0	0	1	0	0	1	1	0	1	3	1	2	3
Dirca palustris	-	-	3	1	0	3	0	0	0	0	1	0	0	1	1	3	1	3	1
Eurybia macrophylla	-	-	2	1	0	3	0	0	1	0	0	1	1	1	2	3	1	2	3
Galium lanceolatum	-	-	2	1	0	3	0	0	1	0	0	0	0	1	1	3	1	2	2
Lysimachia borealis	-	-	1	1	0	3	0	0	1	0	0	0	1	1	2	3	1	2	2
Matteuccia struthiopteris	-	-	3	1	0	3	0	1	0	0	0	0	1	0	2	3	1	1	1
Medeola virginiana	-	-	2	1	0	3	0	0	1	0	0	1	0	1	1	3	1	3	3
Mitchella repens	-	-	1	1	0	3	0	0	1	0	0	1	0	1	2	3	1	2	2

Appendix C. Concluded

			MH	RH	ST	LC	GS	FE	FO	VI	SH	VP	AD	BD	DS	LR	SS	TD	PA
No change																			
Oclemena acuminata	-	-	2	1	0	3	0	0	1	0	0	0	1	0	1	3	1	2	3
Onoclea sensibilis	-	-	3	1	0	3	0	1	0	0	0	0	1	0	2	2	1	1	1
Osmundastrum cinnamomeum	-	-	3	1	0	3	0	1	0	0	0	0	1	0	2	3	1	2	1
Prunus virginiana	-	-	5	1	0	3	0	0	0	0	1	1	0	1	1	2	1	1	3
Pteridium aquilinum	-	-	2	1	0	3	0	1	0	0	0	1	1	0	2	1	1	1	2
Sanicula marilandica	-	-	3	0	0	3	0	0	1	0	0	0	0	1	1	2	1	2	2
Streptopus lanceolatus	-	-	2	1	0	3	0	0	1	0	0	1	0	1	1	3	1	2	3
Uvularia grandiflora	-	-	2	1	0	3	0	0	1	0	0	1	0	1	1	3	1	2	3
Viola canadensis	-	-	1	1	0	3	0	0	1	0	0	1	0	1	1	3	1	2	2

Appendix D

Geographical coordinates of the 133 vegetation plots sampled at Mont-Saint-Bruno National Park in 2013

Plot	Longitude	Latitude	Plot	Longitude	Latitude	Plot	Longitude	Latitude	Plot	Longitude	Latitude
2.2	-73.33667	45.543081	**5.11**	-73.329718	45.55278	**7.13**	-73.324462	45.553535	**9.4**	-73.317995	45.539781
2.3	-73.336975	45.543911	**5.12**	-73.329657	45.553402	**7.14**	-73.324447	45.554448	**9.5**	-73.318133	45.540776
3.1	-73.333321	45.541965	**5.13**	-73.329726	45.553892	**7.15**	-73.324444	45.555277	**9.6**	-73.318084	45.54139
3.2	-73.333366	45.542794	**6.1**	-73.325829	45.535007	**7.16**	-73.324419	45.555858	**9.7**	-73.318082	45.541954
3.3	-73.333644	45.544454	**6.2**	-73.326118	45.53723	**7.17**	-73.324464	45.556671	**9.8**	-73.318055	45.542916
3.4	-73.333641	45.545582	**6.3**	-73.326139	45.538068	**7.18**	-73.324722	45.557235	**9.9**	-73.318336	45.54363
3.5	-73.333612	45.547506	**6.4**	-73.326948	45.551382	**8.2**	-73.320831	45.533274	**9.10**	-73.318335	45.544211
4.1	-73.33085	45.539464	**6.5**	-73.327039	45.552345	**8.3**	-73.320943	45.535032	**9.11**	-73.318318	45.545836
4.2	-73.330845	45.541123	**6.6**	-73.326966	45.553074	**8.4**	-73.321009	45.536476	**9.12**	-73.318906	45.546401
4.3	-73.331147	45.542716	**6.7**	-73.326942	45.553323	**8.5**	-73.321124	45.537521	**9.13**	-73.318343	45.547222
4.4	-73.331145	45.54333	**6.8**	-73.327245	45.554435	**8.6**	-73.321096	45.538881	**9.14**	-73.318635	45.54806
4.5	-73.331142	45.544458	**6.9**	-73.327219	45.555298	**8.7**	-73.3214	45.539728	**9.15**	-73.318632	45.548873
4.6	-73.331396	45.546383	**6.10**	-73.327194	45.555845	**8.8**	-73.321113	45.540839	**9.16**	-73.318582	45.549735
4.7	-73.331381	45.547503	**7.1**	-73.323072	45.533617	**8.9**	-73.321416	45.542225	**9.17**	-73.318603	45.550814
4.8	-73.331679	45.550282	**7.2**	-73.323093	45.534447	**8.10**	-73.321961	45.54916	**9.18**	-73.318625	45.551145
4.9	-73.331665	45.55112	**7.3**	-73.323373	45.535492	**8.11**	-73.321676	45.549442	**9.19**	-73.319376	45.552524
4.10	-73.331779	45.552306	**7.4**	-73.32351	45.536836	**8.12**	-73.321951	45.550305	**9.20**	-73.319087	45.554381
5.3	-73.328619	45.539445	**7.5**	-73.323579	45.5375	**8.13**	-73.32196	45.551134	**9.21**	-73.319432	45.557227
5.4	-73.328686	45.540722	**7.6**	-73.323365	45.53808	**8.14**	-73.321958	45.551947	**9.22**	-73.319313	45.55765
5.5	-73.328895	45.541967	**7.7**	-73.323646	45.538628	**8.15**	-73.32196	45.553083	**9.23**	-73.31917	45.558072
5.6	-73.32918	45.54334	**7.8**	-73.323645	45.538927	**8.16**	-73.322463	45.55821	**9.24**	-73.319439	45.558894
5.7	-73.329172	45.545836	**7.9**	-73.324434	45.551121	**8.17**	-73.322463	45.55821	**9.25**	-73.319379	45.559209
5.8	-73.329723	45.547214	**7.10**	-73.324443	45.551951	**9.1**	-73.318356	45.535816	**9.26**	-73.319448	45.559724
5.9	-73.329454	45.550283	**7.11**	-73.324453	45.552507	**9.2**	-73.318327	45.5375	**10.1**	-73.314747	45.536698
5.10	-73.329743	45.552216	**7.12**	-73.324381	45.553062	**9.3**	-73.318058	45.538619	**10.2**	-73.314744	45.537511

Appendix D. Concluded

Plot	Longitude	Latitude	Plot	Longitude	Latitude
10.3	-73.315001	45.538341	**11.10**	-73.312694	45.550713
10.4	-73.315275	45.539444	**11.11**	-73.312772	45.552223
10.5	-73.315009	45.54141	**11.12**	-73.312738	45.5534
10.6	-73.315283	45.544214	**11.13**	-73.312785	45.555292
10.7	-73.315532	45.545815	**11.14**	-73.312793	45.556395
10.8	-73.315566	45.546106	**11.15**	-73.31306	45.557789
10.9	-73.315589	45.546404	**12.1**	-73.307767	45.546665
10.10	-73.31572	45.549673	**12.2**	-73.30668	45.546945
10.11	-73.315811	45.550635			
10.12	-73.315882	45.552377			
10.13	-73.315868	45.553223			
10.14	-73.316092	45.556856			
10.15	-73.316386	45.557222			
10.16	-73.316111	45.558325			
10.17	-73.316391	45.559171			
10.18	-73.316425	45.559677			
11.1	-73.311956	45.540277			
11.2	-73.311951	45.541679			
11.3	-73.311935	45.542798			
11.4	-73.311952	45.543064			
11.5	-73.312494	45.543338			
11.6	-73.312231	45.544441			
11.7	-73.312241	45.545014			
11.8	-73.312241	45.546689			
11.9	-73.31248	45.549286			